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A Study of Insecticide Resistance in Strains of *Drosophila melanogaster* Meig.[1]

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Introduction

The development of strains or races of insects that are resistant to insecticides is a serious obstacle to the progress of chemical pest control. In many cases recommendations at first viewed as offering a permanent solution for an entomological problem have had to be abandoned within a very few years. Until the general relationships governing insecticidal resistance are reduced to an orderly and understandable basis, the permanent solution of an insect pest control problem by chemical treatment is largely an unjustifiable expectation.

Much experimentation has been done on the toxicological and physiological aspects of acquired insect resistance to insecticides, but little has been done on the ecological and genetic aspects of this problem. This study is an attempt to initiate investigation in the two last-named fields.

Since Melander (1914, 1915) first reported insecticide-resistant strains of insects, entomologists have become increasingly aware of the importance of these developed hereditary differences in susceptibility to insecticides. Entomological literature on the subject is accumulating so rapidly that any biographical listing is rapidly outmoded. Babers (1949, 1951) has listed the most significant general references on the subject. Notable from a genetic standpoint are the works of Hough (1928, 1929, 1934), Dickson (1941), and Knipling (1942). The studies on bacterial resistance to penicillin and bacteriophages by Demerec (1945) and by Demerec and Fano (1945) offer an important groundwork for a genetical approach, although not dealing specifically with insects. The works of Thorpe (1930, 1931) and Smith (1941) ably present the biological race question for zoologists and evolutionists.

A number of fundamental questions regarding acquired resistance to insecticides by insects remain unanswered: How common in natural populations of insects are the factors of resistance to insecticides? Does resistance develop in steps and thus increase continuously as long as the species is subjected to selection by treatment? What genetic arrangements govern the inheritance of resistance factors?

The most obviously useful species for supplying answers to these questions is that of *Drosophila melanogaster* Meig., the physical and genetic diversity of this insect having been subjected to closer scrutiny than that of any other species of animal. The possibility of utilizing *Drosophila* for resistance studies was recognized some time ago. Boyce (1928) used this species in attempts to determine the extent of resistance to hydrocyanic acid gas (HCN) that could be built up in a single strain. He used a wild, heterogeneous strain and compared its resistance to HCN with that of the progeny of a strain developed from selected survivors of seven successive generations, each of which was similarly exposed to HCN.

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An increased survival of treated stock over untreated stock was noted, but the difference was not of such magnitude as to warrant further experimentation.

From a study of the literature it would appear inadvisable to attempt to procure a greatly differing, resistant strain from a relatively homogeneous strain of *D. melanogaster* by laboratory selection. However, Dobzhansky (1937) has presented evidence (1) that many genetic variations arising in the past as mutations in natural populations of *Drosophila*, not subject to positive selection in nature, are retained by the species as incipient variants if suitable conditions are encountered; and (2) that such mutants exist in larger proportions in some strains than others.

Materials and Methods

For the purpose of the present study, stocks of *Drosophila melanogaster* were procured from diverse areas, so that the chance of encountering resistance in some of the stocks might be enhanced. Five strains of *D. melanogaster* were obtained from the Department of Genetics at the California Institute of Technology in Pasadena, through the courtesy of A. H. Sturtevant; five were obtained from the Division of Plant Genetics at the University of California, Berkeley, through the courtesy of E. R. Dempster; and five were collected from other areas in California. One stock was set up as a composite (Σ) stock including equal complements of each of the other fifteen stocks.

The following procedure was used in laboratory handling of field-collected material. Adult flies were isolated, and those not representative, taxonomically, of the *D. melanogaster* complex were discarded. Remaining adults were moved to fresh culture jars daily for 5 days, to reduce the hazard of parasitic mites. Propagation was then started on corn meal-molasses medium.

With all the field-collected material, the following type of cross-mating procedure was used to make certain that only pure *melanogaster* strains were used as test material. From each individual stock, five family lines were set up, using a single, mated female for each culture. One male from each of these family lines was mated with a virgin female of known *D. melanogaster*. If the cross-mating was successfully carried on for two generations, the family lines started from the single, mated females were used as representatives of the field strain. Cutting down of field stocks to a single individual no doubt detracted from the variability of the strain, but at the same time represented a type of family selection likely to result in a greater differential of resistance between strains.

An annotated list of the 16 experimental strains used in this study is presented in Table I. Letters designating strains are those used throughout the study to facilitate reporting of results.

The standard recipe for the corn meal-molasses medium used throughout this study was as follows: water, 713 ml.; molasses, 180 grams, corn meal, 100 grams; Moldex solution (10 per cent solution of Moldex-A in 95 per cent ethyl alcohol), 7 ml. These materials, totalling 1 kg., were combined and cooked in a single container for 3 minutes after the onset of general boiling. Whenever a toxicant was included, a like quantity of water was eliminated. Half-pint milk bottles stoppered with cloth-covered cotton plugs were used as culture jars. After cooling, the medium jars were inoculated with yeast. Before re-use, jars were sterilized by oven-heating for 3 hours at 350°F.

Inasmuch as the corn meal-molasses medium was not satisfactory for mass cultures in large containers, and since at least one other medium was required for evaluation of nutritional effects, investigation of other media was undertaken. Canned custard pumpkin proved to be an excellent mass-rearing medium for

D. melanogaster. This method of *Drosophila* culture, with its advantages and limitations, has been reported in detail (Bartlett, 1951). Its use in the present series of experiments was mainly for the purpose of demonstrating the extent to which insecticidal resistance may be due to nutritional causes. It was occasionally

TABLE I
ANNOTATED LIST OF THE 16 STRAINS OF **Drosophila melanogaster** USED IN INSECTICIDE-RESISTANCE STUDIES

Strain			Source of experimental stock	Notes
Symbol	Name	Place of origin		
Σ	Composite		Equal complements of the 15 strains listed	
C	Oak Glen	Oak Glen, Calif.	Apple pomace from Oak Glen, Calif.	Representative of a southern California mountainous habitat; field-collected
E	Corona	Corona, Calif	Trap jar from Corona, Calif.	Representative of a southern California foothill area; field-collected
H	Orinda	Orinda, Calif.	Division of Plant Genetics, Univ. Calif., Berkeley	Representative of northern California coastal area
I	Oregon R-C	Oregon	Division of Plant Genetics, Univ. Calif., Berkeley	Mass-cultured since 1938 (probably contaminated)
J	Canton-S	Canton, Ohio	Division of Plant Genetics, Univ. Calif., Berkeley	Mass-cultured since 1938 (probably contaminated)
K	Canton-S	Canton, Ohio	Division of Plant Genetics, Univ. Calif., Berkeley	Relatively isogenic stock; brother-sister (virgin) matings for 20 generations
L	Oregon R-C	Oregon	Division of Plant Genetics, Univ. Calif., Berkeley	Relatively isogenic stock; brother-sister (virgin) matings for 20 generations
M	Urbana	Urbana, Ill.	Calif. Institure of Technology	
N	Lausanne	Lausanne, Wis.	Calif. Institute of Technology	
O	Swedish-C	Stockholm, Sweden	Calif. Institute of Technology	
P	Cristobal	Cristobal, Panama	Calif, Institute of Technology	
Q	Indio	Indio, Calif.	Dates from Indio, Calif.	Field-collected
R	Sacramento	Sacramento, Calif.	Grapes from Sacramento, Calif.	Field-collected
T	Hollywood	Hollywood, Calif.	Trap jar from Hollywood, Calif.	Field-collected
W	Canton-S	Canton, Ohio	Calif. Institute of Technology	Pure strain

used where large numbers of test animals of uniform age were required, and also in one experiment in which a toxicant solution was added to the medium for larvicidal tests.

For all the tests, flies were taken at random from the rearing containers, preliminary tests having indicated significant differences in the vitality of flies from different containers. Differences were generally correlated with dehydration of the medium, and were most pronounced in HCN fumigation procedures, where dehydration was augmented by the desiccating effect of a 4- to 5-hour period of anaesthesia.

Untreated controls were used in all the preliminary studies, and Abbott's (1925) formula was used to compensate for natural mortality.

Food moisture and air humidity before, during, and after tests were believed to offer the most important sources of variation in tests with *D. melanogaster*. Standardization of moisture conditions was accomplished by adding distilled water to culture jars showing desiccation, by preserving moisture content of jars by the use of tightly packed plugs, by choosing suitable humidity periods for conducting tests, and by holding the animals, when possible, at a near-saturated air humidity during and after tests.

Flies were reared at a constant temperature of 80° ± 2°F. Since age of test flies was demonstrated by Broadbent and Bliss (1936) and by Morrison (1943) to be of importance, all comparative evaluations were run on young flies ranging in age from 1 to 7 days, unless specifically noted in the text. Only simultaneous comparative evaluations for single test periods were used in the present study. Relative comparisons from different tests were not considered valid.

Owing to the number of flies of uniform age required in the successive-generation selection tests, only mated adults could be used. Mating of resistant females with males of unknown genetic heritage was an unavoidable situation which materially retarded the progress of selection.

Development of Intra-Specific Resistance to Contact Insecticides

Drosophila melanogaster has been scrutinized as a prospective contact-insecticide test animal by a number of insect toxicologists. Morrison (1946) described a test method of exposing *D. melanogaster* to a filter paper which had been impregnated with an acetone solution of insecticide. This method, as well as a number of coated-vial and immersion techniques, was extensively tested, but in all such methods the variance was considered too high for the degree of exactitude required.

R. L. Metcalf of the Division of Entomology of the University of California Citrus Experiment Station modified Morrison's (1946) method of studying insecticidal toxicity by comparing the time required for 50 per cent accumulated mortality of *D. melanogaster* with different materials (unpublished work on file at the Citrus Experiment Station, Riverside, California). This method was tested for use in the present study and found to be quite delicate as a procedure for simultaneous comparisons of toxicity. In this method a filter paper 9 cm. in diameter was impregnated with an acetone solution of the insecticide, dried, and placed in the bottom of a petri dish 9 cm. in diameter, which served as a test cage for the insects.

Resistance of Sixteen Strains of Drosophila melanogaster to DDT.—In the present study, 50 to 100 *D. melanogaster* adults aged 1 to 8 days were collected by a suction aspirator into a vial, chilled to inactivation in the freezing compartment of a refrigerator, and placed in a petri dish containing a DDT-impregnated filter paper prepared as described above. A piece of freshly cut apple and a

small dish of cotton saturated with 5 per cent honey solution provided food and liquid. Periodic counts of accumulated mortality were made at regular intervals, and the LD-50 and LD-95 were determined on an exposure-time basis.

Preliminary trials with this test method, using similar DDT dosages, indicated consistent differences between the *D. melanogaster* strains, in the time required for 95 per cent accumulated mortality. Since practically no natural mortality was observed in check containers after 5 days, no controls were considered necessary.

This procedure of unvaried dosage and variable time for a standard mortality was most adaptable for procuring flies that had survived a near-lethal dosage of the toxicant, for resistance selection studies. The test procedure was standardized for this purpose as follows. One milliliter of a standard acetone solution containing 100 μg. of DDT was used to impregnate the filter paper in the petri-dish test unit, this being a dosage which would result in complete mortality of both sexes of the confined flies in 2 to 3 days. When approximately 90 to 95 per cent mortality of confined female flies had occurred, survivors were removed to corn meal-molasses culture jars for propagation. Occasionally, after transfer to rearing jars, all survivors would die as the result of previous DDT exposure. Occasionally, also, because of the very limited number of survivors from a test, it required as many as three to four generations to build the strain back up to a numerical level suitable for re-exposure. These conditions made it impracticable to test all strains simultaneously, and as a result the strains were carried with varying numbers of exposures to resistance selection.

After five successive DDT exposures (or less with some strains), the DDT-selected strains were compared, in replicated pairs, with flies of the original 16 strains of *D. melanogaster* that had never been subjected to DDT exposure. For this comparison, test flies for both the selected and the unselected strains were reared under exactly similar conditions. In these comparisons separate male and female mortality counts were taken. The two counts were combined in analysis of the data, however, since a 50-50 sex ratio generally prevailed and it was believed that an evaluation made on the combined sexes for each strain would be more representative of the characteristic resistance of the strain. In this evaluation procedure, four paired comparisons between selected and unselected stocks of each strain were made, each at a separate time. Mortality counts were taken on each petri dish at 12, 18, 23, 36, 42, 47, 59, and 71 hours, and the mortality-time curve was drawn. From this curve, the LD-50 and LD-95 were determined by interpolation between the two adjoining points on the eye-fitted curve.

Analysis of the paired comparisons indicated that no statistically significant evidence of increased resistance of any single strain could be shown at the LD-50 level with any of the 16 strains of *D. melanogaster* subjected to the DDT selection process. At the LD-95 level, however, statistically significant increases in resistance to DDT were shown to have occurred in the field-collected strains *Q* and *R*. No such statistically significant increases in resistance to DDT could be shown with any of the laboratory-procured strains, from the data available.

It was apparent from the data that comparisons at the LD-95 exposure period were more delicate for discerning small differences than those at the LD-50 exposure period, under the conditions encountered in the present study. This probably occurs, however, only when genetically impure strains are being subjected to study, since Bliss (1935) has shown that there is, ordinarily, considerably more variance in data at the 95 per cent mortality level than at the 50 per cent level.

Data taken from the paired tests described above were used to show differences between the 16 DDT-selected strains of *D. melanogaster* with respect to resistance to DDT. In Fig. 1, the strains are arrayed in order of ascending resistance to DDT, as shown by mean exposure periods (of four replicates), in hours, required for 50 per cent kill (Fig. 1A) and for 95 per cent kill (Fig. 1B). The numerals combined with the strain designations indicate the number of selective treatments to which the stocks had previously been subjected. The chart (mileage-type) indicates whether or not any strain differs significantly from its fellows in susceptibility to DDT on the basis of individual paired comparisons subjected to *t*-test analysis. There appeared to be sufficient reason for not combining the entire variance, as is necessary in an evaluation of analysis of variance, since differing populations with different inherent variance were obviously involved.

Examination of Fig. 1 indicates that statistically significant differences in susceptibility to DDT residues existed between a number of the DDT-selected strains of *D. melanogaster*. Differences were again more pronounced at the LD-95 exposure periods than at the LD-50 exposure periods. Strain *Q-5*, which had been selected for DDT resistance from an original field-collected stock, showed a consistently higher degree of resistance to DDT than any other strain. Strain *K-5*, which had been selected for DDT resistance from a relatively isogenic strain of Canton-*S* stock, appeared to show the most consistent susceptibility to DDT exposure, with the single exception of the nutritionally weak *O-3* strain.

Inasmuch as the magnitude of differences in resistance to DDT was so small between resistant and susceptible strains, no cross-mating studies to determine the mode of inheritance of the DDT-resistance factor were undertaken.

Resistance of Selected Strains to Other Insecticides.—The two strains *Q-5* and *K-O*, which were representative of the extremes of DDT resistance and susceptibility, respectively, in the 16 strains, were examined further to determine whether the resistance to DDT shown by these strains would carry over to isobornyl thiocyanoacetate,[3] a contact insecticide having a high vapor pressure. The impregnated filter paper-petri dish unit was employed. Flies were reared under identical conditions and were 1 to 5 days old at the time of testing. Sexes were combined in evaluation counts. Counts were made after 18 hours' exposure. Dosages used for impregnation of filter paper were 10 mg. of the commercial isobornyl thiocyanoacetate preparation in 1 ml. of acetone solution, and 100 μg. of DDT in 1 ml. of acetone solution. Paired comparisons with the two materials and with the two strains of *D. melanogaster* resulted in a mean difference of 58.6 ± 5.7 per cent mortality between the two strains, when exposed to DDT. This difference was significant at the 1 per cent level. The mean difference between the two strains when exposed to isobornyl thiocyanoacetate was 20.7 ± 11.0. This difference was not significant at the 5 per cent level.

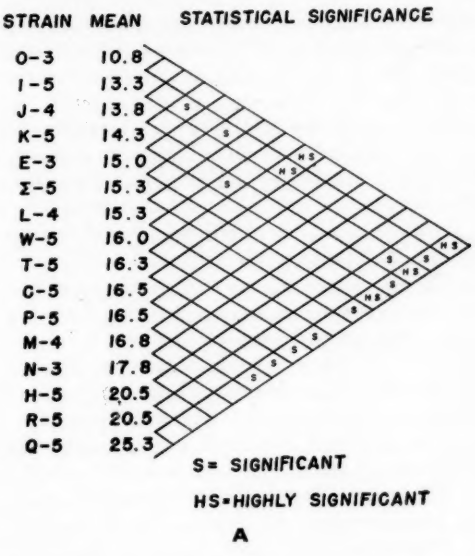
Data collected by R. L. Metcalf indicated that the difference in resistance to DDT between strains *Q-5* and *K-0* carried over to 2,2-bis-(*p*-fluorophenyl) 1,1,1-trichloroethane (DFDT), when tested on a group-comparison basis with 1 mg. of toxicant per milliliter of acetone solution on a filter paper 9 cm. in diameter used according to the filter paper-petri dish method.

Development of Intra-specific Resistance to a Stomach Poison

Four instances of the development of resistance to stomach poisons by insect pests have been recorded. In each, the degree of resistance was very pronounced.

3*Thanite*, a commercial product of the Hercules Powder Company, containing isobornyl thiocyanoacetate (82 per cent) and other active terpenes (18 per cent).

Where noted as a field phenomenon, the developed resistance was of such magnitude as to cause abandonment of control measures with the particular insecticidal material used (Hough, 1928; Boyce *et al.*, 1942; Du Toit *et al.*, 1941). In the one



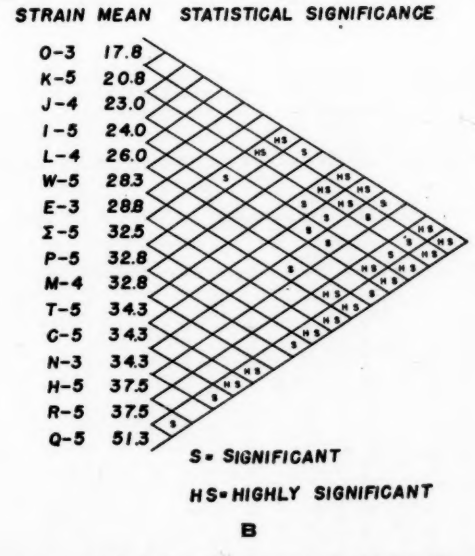


Fig. 1. Mean exposure periods (in hours) required (A) for 50 per cent mortality and (B) for 95 per cent mortality of 16 DDT-treated, selected strains of *Drosophila melanogaster*, showing strains in ascending order of resistance to DDT. (Numerals combined with strain designations indicate number of selective treatments to which stocks had previously been subjected.) Significant differences between strains in susceptibility to DDT, according to *t*-test analysis of four paired comparisons, are shown in the mileage-type tables.

example recorded from the laboratory, namely, that of the resistance of *Cochliomyia americana* C. and P. to phenothiazine, the degree of resistance was again very marked (Knipling, 1942). Resistance was shown in these reports to be identified with adults or larvae or, occasionally, with both.

Methods employed by Knipling (1942) suggested that similar methods might be applicable for testing resistance of *Drosophila melanogaster* to tartar emetic (potassium antimonyl tartrate). Since this material forms a true solution in water, it appeared possible that adult tests, as well as larval tests, might be made on the poisoned medium. The utilization of such a poisoned-medium test technique would be expected to provide two features most desirable for a satisfactory test procedure: namely, a method of administering uniform dosages and, provided sex mortality differences were not evident, a method of selection wherein resistance-selected females would be mated only with resistance-selected males. It is thought that both of these objectives were realized with the method used.

Comparative Resistance of the Sixteen Strains to Tartar Emetic.—Culture jars made up with corn meal-molasses medium containing 0.2 per cent tartar emetic were permitted to dry out for 24 hours prior to use. Twenty-five females and 25 males were introduced into each jar with a suction pipette. Those still alive after 7 days were removed from the jars. Daily counts were made of the progeny of these flies as they emerged. Surviving progeny were cultured on unpoisoned medium for two to three generations, and the strain was again subjected to a similar tartar-emetic selection test, using a 0.1 per cent higher dosage increment. All strains were run concurrently on medium from a single batch, to minimize environmental differences. If no survivors were available from the test with a certain strain, the strain was tested again with the next dosage increment before being eliminated from the series. Dosages of tartar emetic were

TABLE II

AVERAGE NUMBERS OF PROGENY OF EACH SEX EMERGING PER JAR FROM ADULTS OF SIXTEEN STRAINS OF *Drosophila melanogaster* SURVIVING TREATMENT WITH INCREASING CONCENTRATIONS OF TARTAR EMETIC*

	NUMBER OF FLIES AT GIVEN CONCENTRATION OF TARTAR EMETIC IN MEDIUM											
	0.2 per cent		0.3 per cent		0.4 per cent		0.5 per cent		0.6 per cent		0.7 per cent	
Strain	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Σ	12	29	3	9	0	0	1	1.4	0.2	1.2	0	0.3
C	2	5	9	9	0	0	0	0				
E	1	4	6	7	0	0.5†	0	0				
H	19	26	14	13	1.8	1.5	1.6	2.9	1.4	1.3	1.8	3.5
I	0	0	0	0								
J	8	18	2	6	0	0	0	0				
K	10	9	6	8	0	0	0	0				
L	0	0	0	0								
M	10	17	6	2	0	0.5†	0	0				
N	0	0	0	0								
O	1	1	1	0	0	0	0	0				
P	9	3	0	0	0	0						
Q	34	33	5	7	0	0	0	0.3†	0	0		
R	17	11	9	9	0	0	0	0				
T	35	27	15	17	0	0.5	7	2	1.3	1.2	1.5	2
W	19	13	12	16	0	0	0	3.†	0.6	0.9	2.8	1.3

* Evaluation at successive concentrations of tarter emetic based on the numbers of flies emerging from eggs laid by 25 female progeny of survivors of treatment at preceding, lower dosage.
† Mated with males of a preceding test.

increased form 0.2 per cent through 0.7 per cent. At the higher dosages the number of test jars for each strain was increased to guard against loss of the strains. The average numbers of progeny of each sex emerging per test jar are recorded in Table II.

The results of selections for tartar emetic resistance through both larval and adult stages of 16 strains of *D. melanogaster* (Table II) indicate that under the conditions of these tests there were differences in resistance to tartar emetic between the strains.

Comparative Resistance of Larvae and Adults of Tartar Emetic—Resistant and Nonresistant Strains.—Separate tests were designed to compare the resistance exhibited (1) by the larvae and (2) by the adults of the tartar emetic-resistant strain *H*-7 and of the nonresistant strain *L*.

For tests on larval susceptibility of the two strains to tartar emetic, 10 jars of corn meal-molasses medium poisoned with 0.4 per cent tartar emetic were used. Fifty first-instar larvae of each strain were transferred by means of a sterile needle directly from unpoisoned medium to each of five jars. Counts of emerging adults showed a total of 6 males and 7 females emerging from the five jars infested with larvae of the *H*-7 strain, and a total of 2 males and 0 females from the five jars infested with the larvae of the nonresistant *L* strain. Data from this test, when compared with that taken earlier on *L* stock, indicated that the stock may have become contaminated in the course of handling, but larval resistance was still more pronounced in the *H*-7 strain than in the *L* strain.

For tests on susceptibility of adults of the two strains to tartar emetic, six jars of medium containing 0.4 per cent tartar emetic were prepared, and 25 adult males and 25 adult females, aged 1 to 8 days, were placed in each jar. Mortality counts were made at 24-hour intervals on each jar for 8 days, with separate sex

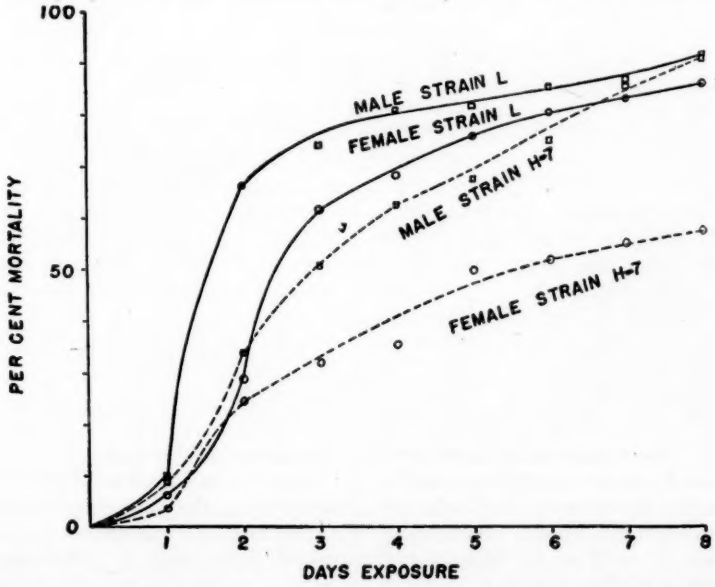


Fig. 2. Comparative mortality curves for adult males and females of a strain of *Drosophila melanogaster* resistant to tartar emetic (*H*-7) and of a nonresistant strain (*L*) when exposed to tartar emetic medium continuously for 8 days.

counts. In Fig. 2 are presented separate time-mortality curves for the 150 males and 150 females of each strain over the 8-day period.

The total effective egg-laying periods for adult females of the *H*-7 strain before death were calculated from the survival data to be 735 fly-days, compared with 466 fly-days for those of the *L strain*. The LD-50 exposure period for females of the *H*-7 strain was 5 days, and for those of the L strain, 2½ days.

Records were kept of the total progeny emerging in the previous tests from the jars containing tartar emetic-poisoned medium. The total number of males emerging from the six jars infested with *H*-7 strain was 120, and of females was 146; from the six jars infested with *L* strain, there emerged 3 males and 1 female. Assuming equal fecundity in the two strains, and compensating for the lesser number of days available for egg-laying by females of the *L* strain, there was still forty times as great a survival of larval forms in strain *H*-7 as in strain *L* at the dosage level tested.

Although some contamination of *L* strain was indicated, tests were set up to try to determine the genetic results of reciprocal crosses between the nonresistant *L* strain and the tartar emetic-resistant *H*-7 strain. For this comparison of the two strains and their hybrids, 0.4 per cent tartar emetic medium was used. This high concentration of tartar emetic was used in order to counteract the possibility of contamination in the nonresistant *L* strain. Tests were made with mass crosses, using 15 virgin females and 15 males per jar. Fifteen virgin females were used per jar for the control crosses of pure stocks. All crosses were replicated seven times. Parental stocks still remaining alive at the end of 8 days were removed from jars. Counts of emerging progeny from the seven replicate jars for each cross are shown in Table III. Results of these crosses are considered too incomplete to demonstrate the mode of inheritance of tartar emetic resistance in hybrids between the two strains.

TABLE III

PROGENY OF RESISTANT (H-7) AND NONRESISTANT (L) STRAINS OF *Drosophila melanogaster* AND THEIR RECIPROCAL CROSS MATINGS WHEN REARED ON MEDIUM CONTAINING TARTAR EMETIC (0.4 PER CENT)

Strains crossed (Females x Males)			Average number of adult progeny	
			Females	Males
H-7	x	H-7	28	12
H-7	x	L	1	1
L	x	H-7	16	6
L	x	L	2	1

Development of Intra-specific Resistance to Fumigants

A study of the 16 different strains of *Drosophila melanogaster* with respect to their varying resistance to HCN was undertaken for the purpose of acquiring two intra-specific strains representing the extremes of resistance and nonresistance, as well as to determine the natural occurrence of conditions of resistance in various strains.

The work of Dickson (1941), in which resistant and nonresistant strains of California red scale were crossed, indicated the resistance factor to HCN in that

insect to be inherited as a sex-linked character with incomplete dominance, and suggested the possibility that only a single gene might be involved.

Isolation of HCN-resistant and nonresistant strains of *D. melanogaster*, would provide interesting comparisons with HCN resistance in red scale, and would permit further studies of both a physiological and a genetic nature, which are difficult with scale insects.

Resistance of the Sixteen Strains to Fumigation with HCN.—Apparatus especially constructed for HCN test fumigation was available for these experiments. A gastight fumatorium having a capacity of 100 cu. ft. and fitted with a circulating system and temperature control was used. A small trap in the top of the system permitted removal of an exposed test cage of insects without disturbing the existing concentration in the chamber. Dosage curves may thus be presented on the basis of exposure time at a constant gas concentration. Inasmuch as *D. melanogaster* adults are very sensitive to moisture requirements, and adequate humidity control was not available in the fumatorium, duplication of mortality results at different times was difficult. In all tests, therefore, toxicity comparisons must be considered as relative only within the same exposures. Since mortalities for any anticipated exposures were unpredictable from one time to the other, whenever possible series of dosages were run concurrently, so that the desired mortality range would be encountered. Approximately 95 to 98 per cent kill was desired for resistance selection tests, to eliminate the susceptibility factor.

Cylindrical test cages 6 inches long and 3 inches in diameter, constructed of celluloid and designed so they could be pulled apart in the centre, were used in the fumigation experiments. Each end of these cages was covered with 40-mesh bronze screening. A cotton-plugged hole $\frac{3}{8}$-inch in diameter, through one screen, served for the introduction and removal of flies.

The greatest care was taken to see that test animals were maintained always in a moist environment prior to, during, and after fumigation. The culture medium was kept at a near-optimum moisture content prior to utilization of adults for test purposes. When the insects were being prepared for testing, and during fumigation, a fresh slice of apple was always present in each test cage for food and liquid, and all cages were exposed, as nearly as possible, to uniform temperature and humidity conditions. After fumigation the contaminated pieces of apple were replaced by fresh slices, and the cages were held in a room maintained at a relative humidity of 80 to 90 per cent and at a temperature of 80°F. for 6 hours before counting. Since HCN is a powerful insect anaesthetic, a few moments' exposure to the HCN concentrations used in this study were enough to inactivate the test animals for several hours. This period was often critical if the humidity was low and moisture was not available to the flies. With adequate precautions, however, check mortality was consistently less than 1 per cent.

Preliminary tests using *W*-strain adults aged 1 to 8 days indicated that exposure to a dosage of 2 ml. of HCN per 100 cu. ft. resulted in 50 per cent mortality in 15 minutes and 100 per cent mortality in 40 minutes. The test conditions were therefore standardized for all evaluations at a dosage of 2 ml. HCN per 100 cu. ft., using flies 1 to 8 days old. Under these conditions mortality counts made at three dosage levels demonstrated that there was no significant variation in kill between males and females of *D. melanogaster* with HCN fumigation.

In the first two comparative test operations, the process of selection from successive generations for resistance to HCN fumigation was combined with the process of evaluation of resistance of the 16 strains to the fumigant. In the three

comparisons that followed, the strains of intermediate resistance demonstrated by the preceding two tests were eliminated from consideration, since it was impossible to carry and test all the stocks at the numerous dosage variations required for a high degree of selection.

In the first two comparative test operations, the process of selection from strains reared on corn meal-molasses medium and on canned pumpkin medium, to determine differentials due to nutrition. Results of comparisons of the 16 strains reared on these two media and fumigated for 30 minutes at 75°F. and 42 per cent relative humidity, with 2 ml. of HCN per 100 cu. ft., are presented in Table IV. In the same table are presented results of a second test on the various strains after one selective fumigation exposure.

TABLE IV

COMPARATIVE MORTALITY OF 16 STRAINS OF *Drospohila melanogaster* WHEN REARED ON TWO DIFFERENT MEDIA AND FUMIGATED WITH 2 ML. HCN PER CUBIC FEET (EXPOSURE, 30 MINUTES AT 75° F. AND 42 PER CENT RELATIVE HUMIDITY)

Strain	Series 1 (Unselected strains reared on corn meal-molasses medium)		Series 2 (Unselected strains reared on canned pumpkin medium)		Series 3 (Once-selected strains reared canned pumpkin medium)	
	Flies tested	Per cent mortality	Flies tested	Per cent mortality	Flies tested	Per cent mortality
Σ	806	91.6	206	83.5	476	91.6
C	204	88.2	208	72.6	294	96.0
E	212	84.4	99	79.8	280	89.6
H	369	93.8	592	99.0	109	100.0
I	293	52.6	145	83.4	225	75.1
J	237	91.1	209	96.7	129	81.4
K	205	79.5	293	98.3	361	97.0
L	364	27.2	206	63.1	197	74.1
M	280	77.5	349	97.7	235	87.7
N	274	100.0	225	100.0	225*	100.0
O	231	90.5	191	97.9	245	98.4
P	171	93.0	177	79.7	107	94.4
Q	179	56.4	203	74.4	224	91.5
R	272	90.4	182	79.7	251	96.0
T	257	83.7	206	89.3	430	91.2
W	151	97.4	339	91.7	437	86.5

* Unselected strain substituted, since there were no survivors from prior tests.

The data of Table IV indicate consistent differences in resistance to HCN fumigation between the 16 strains of *D. melanogaster* tested, with relatively little observed change, whether the insects were reared on a medium of corn meal and molasses or of canned pumpkin. Strain *N* showed a consistently lower resistance to fumigation with HCN than the other strains. Strain *L*, a relatively isogenic stock of Oregon *R-C*, showed consistently higher resistance to this fumigant than the other strains. Strain *I*, a mass-cultured stock of Oregon *R-C*, also showed a high degree of resistance. The composite stock Σ showed a degree of resistance to HCN somewhat intermediate between other strains.

Resistance of Selected Strains to Fumigation with HCN.—For the remaining fumigation selection series, all strains except the resistant *L*, the nonresistant *N*, and the composite stock Σ were discontinued. For succeeding selection exposures, the strains were reared alternately on canned-pumpkin medium for one exposure and then on corn meal-molasses medium for the next exposure. When four exposures of the *L* stock and five exposures of the Σ stock had been

completed, limited comparative tests were conducted to determine whether or not progress was being made in the selection for HCN resistance.

Comparative results with the two strains of *D. melanogaster* reared on the two different media and fumigated for 30 minutes at 80°F. and 50 per cent relative humidity, with 2 ml. HCN per 100 cu. ft., are presented in Table V. From these results, it is apparent that the progress of selection for resistance to HCN was proceeding at a very slow rate, even with the composite (Σ) strain. Also, contamination of the *N* stock had been indicated in the last two selection fumigations, where the nonresistant (*N-0*) stocks had been compared with the *L-2* and *L-3* selection exposures. Because of these facts it was considered advisable to go ahead with the projected studies of the HCN-resistant (*L-5*) and nonresistant (*N-0*) strains, despite their suspected heterogeneity with respect to HCN resistance.

TABLE V

EFFECT OF REARING MEDIA AND OF PRIOR SELECTIVE FUMIGATION WITH HCN ON RESISTENCE OF TWO SELECTED AND TWO UNSELECTED STRAINS OF *Drosophila melanogaster* TO FUMIGATION WITH 2 ML. HCN PER 100 CU. FT. (EXPOSURE, 30 MINUTES AT 80° F. AND 50 PER CENT RELATIVE HUMIDITY)

Strain and No. of prior selective fumigations	SERIES 1 Reared on corn meal-molasses medium)		SERIES 2 (Reared on canned pumpkin medium)	
	Flies tested	Per cent mortality	Flies tested	Per cent mortality
Σ–0	65	96.9	187	81.3
Σ–5	173	94.2	524	72.1
L–0	123	93.4	356	54.8
L–4	268	77.6	308	53.6

Before proceeding with dosage-mortality comparisons of the extreme resistant *L* strain, survivors of higher dosages from the *L-4* and Σ-*5* stocks were propagated to give *L-5* and Σ-*6* stocks, and these were compared again in a single fumigation exposure to Σ-*0* stock. Results with these stocks, reared on a medium of corn meal and molasses and fumigated for 40 minutes at a temperature of 60°F. and 33 per cent relative humidity, with 2 ml. HCN per 100 cu. ft., were as follows: with 241Σ-*6* adults, 64.3 per cent mortality; with 283Σ-*0* adults, 81.6 per cent mortality; with 122 *L-5* adults, 57.0 per cent mortality. A single fumigation of adult HCN-resistant (*L-5*) and nonresistant (*N-0*) strains reared on corn meal-molasses medium was conducted to procure comparative dosage-mortality curves. Data from fumigation of the two strains with various dosages of HCN at 60°F. and 33 per cent relative humidity are presented in graphical form in Fig. 3.

Hybrid progeny resulting from reciprocal crosses between the HCN-resistant (*L-5*) strain and the nonresistant (*N-0*) strain were compared in susceptibility to HCN fumigation, along with the progeny resulting from regular crosses within ecah strain, in an attempt to determine the method of inheritance of the resistance factor. Seven jars of corn meal-molasses medium were set up for each cross. Five unmated females and five males were used as parental stock in each jar, and 1- to 7-day-old progeny of the four crosses were used for the comparative tests.

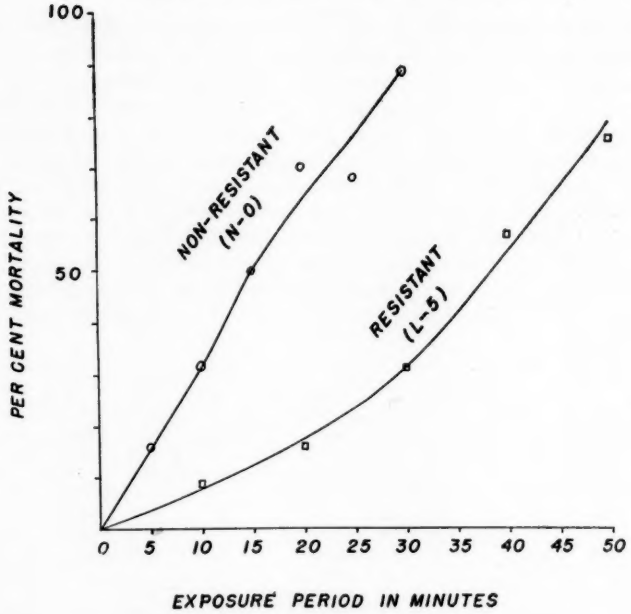


Fig. 3. Dosage-mortality relationship between HCN-resistant (*L-5*) and nonresistant (*N-0*) strains of *Drosophila melanogaster*.

Fumigation was conducted at a temperature of 75°F. and at 23 per cent relative humidity, using 2 ml. HCN per 100 cu. ft., for an exposure of 45 minutes. Results, which are presented in Table VI, indicate that some contamination of the *N-0* strain had probably occurred, as demonstrated by some survival even at the excessive HCN dosage used in the test. From these limited data, no evidence could be shown for sex-linkage of the HCN-resistance characteristic.

Resistance of Selected Strains to Cold and to Fumigation with Diethyl Ether.—The HCN-resistant strain *L-5* was compared with the HCN-nonresistant

TABLE VI

RESISTANCE TO HCN FUMIGATION EXHIBITED BY F1 OF HCN-RESISTANT (L–5) AND NONRESISTANT (N-O) STRAINS OF *Drosophila melanogaster* AND BY THE F1 OF THEIR RECIPROCAL CROSS-MATINGS

Strains crossed (female x male)	F1 PROGENY			
	Males		Females	
	Total number	Per cent mortality	Total number	Per cent mortality
L–5 x L–5	207	95.2	226	96.5
N–O x N–0	122	100.0	153	99.3
L–5 x N–0	68	97.1	67	98.5
N–O x L–5	80	96.3	105	94.3

strain *N-0* for resistance to cold. In preliminary tests, 10 hours' exposure to a temperature of 40°F. was found insufficient to cause appreciable mortality in either strain; however, a notable difference was apparent between the strains in the period of recovery from cold rigor. Five minutes after removal to a temperature of 80°F. only 3.8 per cent of the flies of the *N-0* strain had recovered, and 22.9 per cent of the *L-5* strain had recovered. After 30 minutes, only 28 per cent of the *N-0* strain and 98 per cent of the *L-5* strain had recovered.

Tests of the comparative resistance to cold of the two strains were conducted by exposing flies 1 to 7 days old to a temperature of approximately 10°F. for 75 minutes in the freezing compartment of an electric refrigerator. The flies were placed in open-end glass tubes measuring 22 x 85 mm. The ends of the tubes were covered with 40-mesh bronze wire. Four paired comparisons were made with alternate randomization of the positions of the tubes. Counts were made 24 hours after exposure. The mean difference between the two strains of *D. melanogaster* with respect to cold survival was 42.6 $\pm$ 3.8 per cent, which was highly significant. Strain *L-5*, which had previously exhibited resistance to HCN exposure, was also resistant to low temperatures. In the course of this comparison a difference between the two strains was again evident with respect to time of recovery from cold rigor. Flies of the *L-5* strain recovered more quickly than those of the *N-0* strain.

Resistance of the same two strains of *D. melanogaster* to fumigation with diethyl ether was also studied. A stopper-topped bell jar of 3-liter capacity was used as a fumatorium. Three milliliters of diethyl ether were introduced into the bell jar by pouring the ether onto a cotton ball affixed to the under side of the stopper. Tests were conducted with a uniform concentration and varying exposure periods. No circulation of the volatilized ether within the bell jar was attempted. Eight paired comparisons were made of the two strains. Glass tubes 22 mm. in diameter and 85 mm. long, covered on either end with 40-mesh bronze screening and placed under a bell jar, served as test-unit cages. Randomized flies aged 1 to 7 days were used in the comparison. For these tests, the exposure period ranged between 18 and 24 minutes. Counts were made 18 hours after exposure.

A highly significant difference between the two strains in susceptibility to diethyl ether fumigation was shown, with a mean difference of 28.4 $\pm$ 8.2 per cent and higher resistance in strain *L-5* than in strain N-0. It was apparent in these tests that there were also pronounced differences between the two strains with respect to recovery period from the anaesthetic action of the ether, flies of the *L-5* strain recovering more quickly than those of the *N-0* strain.

Summary

Sixteen strains of *Drosophila melanogaster* representative of diversified climate and food habits were assembled from laboratory and field sources. These strains of *D. melanogaster* were isolated as family lines and tested for extent of susceptibility to DDT, a contact poison; tartar emetic, a stomach poison; and to hydrocyanic acid gas, a respiratory poison. Suitable test methods for adequate evaluation of small differences in susceptibility between the 16 strains were developed.

Difference in insecticidal resistance between strains of *D. melanogaster* was demonstrated to occur in treatment with DDT, tartar emetic, and HCN. Resistance was shown to be inherited and not associated with nutrition. The use of successive selective insecticidal treatments resulted in increased resistance in some strains, but not in others. The rate of increase in resistance to DDT and HCN

following successive selective treatments of populations of *D. melanogaster* was found to be very slow. Evidence of more than one level of DDT resistance in relatively isogenic strains suggests that this resistance develops in steps. Resistance to DDT and HCN was tested with adult flies only. Resistance to tartar emetic was demonstrated in both adult and larval stages but was more pronounced in the larval stage. A number of strains of *D. melanogaster* were markedly resistant to tartar emetic. This resistance was not specific for tartar emetic alone, but carried over to a certain degree to DDT and to HCN.

Resistance by the strain most highly resistant to HCN was shown to have some specificity for HCN, since it was resistant neither to DDT nor to tartar emetic. Adult flies of this strain were shown, however, to be resistant to diethyl ether and to a subfreezing temperature (10°F.), as well as to anaesthesia induced from either of these two treatments. Inheritance of HCN resistance was indicated as being without sex-linkage.

The strain of *D. melanogaster* showing greatest resistance to DDT treatment was also highly resistant to DFDT, moderately resistant to HCN and tartar emetic, and slightly if at all resistant to isobornyl thiocyanoacetate.

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Mallophaga Collected from Birds in Ontario

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It is difficult to obtain accurate records of the occurrence of bird-lice and especially those associating them with correctly identified hosts. For this reason it is considered the following records of bird-lice, taken from birds in Ontario, may be of interest and should be published.

The collections were made by the author and Messrs. A. A. Wood and D. A. Arnott and one or two other persons. The specimens are in the collection of the Dominion Entomological Laboratory, Chatham, Ontario.

The bird-lice were kindly identified for the author by Dr. E. W. Stafford of Mississippi State College. The birds were identified by the author or Mr. A. A. Wood.

List of Species, with Hosts, Place of Collection and Date

FAMILY MENOPONIDAE

Trinoton querquedulae (L.)
Lesser Scaup, *Aythya affinis*, Paincourt, April 28, 1940
Red-breasted Merganser, *Mergus serrator*, Erieau, April 27, 1943
Wood Duck, *Aix sponsa*, Paincourt, November 3, 1943

Actornithophilus subpustulatum (Carriker and Shull)
Belted Kingfisher, *Megacercyle alcyon*, Paincourt, September 8, 1944

Actornithophilus minus (K)
Dowitcher, *Limnodromus griseus*, two specimens, Paincourt, September 3, 1945
Semipalmated Sandpiper, *Ereunetes pusillus*, Paincourt, September 5, 1945

Menacanthus praecursor (K)
Common Sapsucker, *Sphyrapicus varius*, Chatham, April 22, 1944

Menacanthus spinosus (Piaget)
Starling, *Sturnus vulgaris*, Chatham, April 22, 1944
Olive-backed Thrush, *Hylocichla ustulato*, Kent County, May 19, 1941

Menacanthus chrysophaeus (K)
Yellow-breasted Chat, *Icteria virens*, Paincourt, May 21, 1940

Menacanthus sp.
Common Goldfinch, *Spinus tristis*, Kent Bridge, no date

Myrsidea americana (K)
Common Crow, *Corvus brachyrhynchos*, Jeannettes Creek, February 15, 1944

Myrsidea incerta (K)
Hermit Thrush, *Hylocichla guttata*, Newburg, Middlesex County, October 12, 1942

Colpocephalum flavescens (Nitzsh)
Bald Eagle, *Haliaeetus leucocephalus*, Paincourt, October 22, 1943

Colocephalum osborni (K)
Bald Eagle, *Haliaeetus leucocephalus*, Paincourt October 22, 1943
Colocephalum subpachygaster (Piaget)
Great Horned Owl, *Bubo virginianus*, Kent County, no date
Colpocephalum sp.
Red-tailed Hawk, *Buteo jamaicensis*, Port Stanley, Elgin County
Colpocephalum sp.
Short-eared Owl, *Asio flammeus*, Cedar Springs, no date
Colpocephalum laticeps (K)
Black-bellied Plover, *Squatarola squatarola*, Paincourt, September 7, 1944
Kurodaia haliaeti (Denny)
Sora, *Porzana carolina*, Paincourt, September 8, 1942

FAMILY RICINIDAE
Ricinus picturatus (Carr)
Cape May Warbler, *Dendroica tigrina*, Chatham, May 14, 1941

FAMILY LAEMOBOTHRIIDAE
Laemobothrion titan (Piaget)
Bald Eagle, *Haliaeetus leucocephalus*, Paincourt, October 22, 1943

FAMILY PHILOPTERIDAE
Philopterus corvi (Packard)
Common Crow, *Corvus brachyrhynchos*, Jeannette's Creek, February 15, 1944
Philopterus subflavescens (Geoffroy)
Ovenbird, *Seiurus auracapillus*, Paincourt, May 18, 1944
Common Snow Bunting, *Plectrophenax nivalis*, Jeannette's Creek, January 12, 1943
Horned Lark, *Otocoris alpestris*, New Glascow, Elgin County, February 4, 1943 and Chatham, March 21, 1940
Philadelphia Vireo, *Vireo philadelphicus*, Chatham, May 25, 1943 and May 22, 1944
Cooper's Hawk, *Accipiter cooperii*, Kingsville, Essex Co., January 18, 1945
Swamp Sparrow, *Melospiza georgiana*, Paincourt, May 9, 1945
Myrtle Warbler, *Dendroica coronata*, Paincourt, May 9, 1945
Philopterus domesticus (K)
Purple Martin, *Progne subis*, Paincourt, May 12, 1941
Philopterus excisus major (K)
Tree Swallow, *Iridoprocne bicolor*, Paincourt, May 14, 1945
Philopterus incisus (K)
Golden-crowned Kinglet, *Regulus satrapa*, Kent County, April 17, 1941
Penenirmus californiesis (K)
Red-headed Woodpecker, *Melanerpes erythrocephalus*, Chatham, September 15, 1940
Common Sapsucker, *Sphyrepicus varius*, Chatham, April 22, 1941
Penenirmus sturni (Schrank)
Starling, *Sturnus vulgaris*, Chatham, April 22, 1941
Eustrigiphilus syrnii (Packard)
Short-eared Owl, *Asio flammeus*, Paincourt, March 17, 1940
Eustrigiphilus cursor (Nitzsch)
Short-eared Owl, *Asio flammeus*, Cedar Springs, October 16, 1945
Eustrigiphilus ceblebrachys (Nitzsch)
Snowy Owl, *Nyctea scandiaca*, Paincourt, October 24 and 27, 1945 (2

birds), November 6, 9 and 15, 1945 (3 birds)
Great Horned Owl, *Bubo virginianus*, Kingsville, Essex County. No date.
Eustrigiphilus bubonis (Osborn)
Arctic Horned Owl, *Bubo virginianus wapacuthu* (Gmelin), Chatham, January 10, 1942
Great Horned Owl, *Bubo virginianus*, Chatham, November 10 and 30, 1944 (2 birds)
Craspedorrhynchus haliaeti (Osborn)
Bald Eagle, *Haliaeetus leucocephalus* (Audubon) Paincourt, October 22, 1943
Craspedorrhynchus taurocephalus (K)
Red-tailed Hawk, *Buteo jamaicensis*, Chatham, December 21, 1944
Anatoecus dentatus (Scop.)
Red-breasted Merganser, *Mergus serrator*, Erieau, April 27, 1943
Blue-winged Teal, *Anas discors*, Paincourt, April 5, 1940
Lesser Scaup Duck, *Aythya affinis*, Paincourt, April 25, 1940
Scaup Duck *Aythya marila*, Erieau, November 13, 1945
Saemmssonia gonothorox (Giebel)
Herring Gull, *Larus argentatus*, Paincourt, April 12, 1943
Bonaparte's Gull, *Larus philadelphia*, Erieau, June 12, 1945
Saemmssonia fusiformis (Denny)
Semipalmated Sandpiper, *Ereunetes pusillus*, Paincourt, September 3, 1945
Saemmssonia sp.
Dowitcher *Limnodromus griseus*, Paincourt, September 3, 1945 (3 birds)
Quodraceps major (K)
Dowitcher, *Limnodromus griseus*, Paincourt, September 3, 1945
Carduiceps complexiva (K)
Pectoral Sandpiper, *Erolia melanotos*, Paincourt, September 5, 1945
Least Sandpiper, *Erolia minutilla*, Paincourt, September 4, 1945
Anaticola crassicorne (Scop)
Red-breasted Merganser, *Mergus serrator*, Erieau, April 27, 1943
Blue-winged Teal, *Anas discors*, Paincourt, April 15, 1940
Lesser Scaup Duck, *Aythya affinis*, Paincourt, April 25, 1940
American Widgeon, *Mareca americana*, Paincourt, Nov. 28, 1944
Ornithobius cygni (Schrank)
Whistling Swan, *Cygnus columbianus*, Paincourt, November 10, 1942
Columbicola columbae (Linne)
Rock Dove, *Columba livia*, Chatham, July 30, 1944
Brüelia nebulosa (Nitzsch)
Starling, *Sturnus vulgaris*, Chatham, April 22, 1944, Steptember 23, 1943, March 26, 1940. (3 birds)
Brüelia rotundata (Osborn)
Common Crow, *Corvus brachyrhynchos*, Jeannette's Creek, February 15, 1944
Degeeriella fusca (Nitzch)
Red-tailed Hawk, *Buteo jamaicensis*, Merlin, January 24, 1944, and Kent County, December 21, 1944 (2 birds)

The Nearctic Species of *Macrosteles* (Homoptera: Cicadellidae)[1]

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Introduction

The correct identifications of North American species of leafhoppers of the genus *Macrosteles* (sensu lato) are important because of the economic significance of one of them as a carrier of a virus disease of many species of plants. In the past, such identifications have been difficult to make because the extent of the variation in colour, markings, and structure that occurs has not been appreciated fully, because some species were misidentified in previous revisions, and because there were a number of unrecognized species in the fauna.

In the present paper the diagnostic characters of each species or species complex are described and figured, the extent of the variation is discussed, and the distributions and, when known, the habits are described. A total of about 5,800 specimens of *Macrosteles* spp. were examined. They included all the known Nearctic species with a single exception, *M. lineatifrons* (Stål, 1858, p. 195). Eight species are added to the Nearctic list. These comprise four species new to science and four European species not recorded previously for North America. The North American records for two European species are shown to be incorrect. Changes in the specific names of some species are necessary, including that of the economically important six-spotted leafhopper, heretofore known as *Macrosteles divisa.*

M. lineatifrons cannot be recognized with certainty from Stål's description, which could apply to several species found in Alaska. The type has apparently been lost: there are no specimens under this name from the type locality, Sitka, Alaska, in the Stål Collection in the Naturhistoriska Riksmuseum, Stockholm, and the only unidentified leafhoppers from Sitka in that collection were specimens of *Evacanthus acuminatus* (Fab.), which I have examined. The specimens collected by the Harriman Alaskan Expedition at Saldovia that were recorded as *lineatifrons* by Ashmead (1904) are of *salina.* In the absence of the type of *lineatifrons* it is impossible to arrive at any conclusion on the identity of the species.

Macrosteles Fieber

Macrosteles Fieber, 1866: 504. Type, by subsequent designation of Dorst, 1937: 4 and 12, *Cicadula sexnotata* Fall.
Davisonia Dorst, 1937: 4. Type, by original designation, *Cicadula major* Dorst.
Sonronius Dorst, 1937: 9. Type, by original designation, *Cicadula dahlbomi* Zett.
Sagatus Ribaut, 1948: 57. Type, by original designation, *Cicada punctifrons* Fall.

Dorst (1937) apparently mistook European specimens of *fieberi* (Edw.) for *sexnotata* (Fall.). However, this does not alter the status of *sexnotata* as the genotype of *Macrosteles.* Ossiannilsson (1948) gave *dahlbomi* (Zett.) as a synonym of *quadripunctata* (Fall.). Oman (1949) gave the date of publication of Dorst's description on *Sonronius* as 1931, in error for 1937.

Macrosteles (sensu lato) is one of two known Nearctic genera of the tribe Macrostelini of the subfamily Deltocephalinae. The insects of this tribe are macropterous, with long slender fore wings, each fore wing not being straight on the commissural margin from base to apex but having a well-developed appendix, with the outer anteapical cell absent and with the inner anteapical cell open basally; the ocellus is situated near the eye and the genae are not visible from above, and the basal segment of the hind tarsus is not sulcate basally. The

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last character distinguishes the tribe from the closely related Balcluthini. The second genus of the Macrostelini is *Baldulus* Oman. Oman (1934) stated that it differs from *Macrosteles* in having the fore wings long and slender, as in *Balclutha*, and the head narrow, produced, and angled, as in *Deltocephalus*. The colour distinctions given subsequently by Oman (1949) do not hold good. The three known Nearctic species of *Baldulus* occur in the southwestern parts of the United States, one of them also in the southeast.

The species discussed in the present paper were included in the genus *Cicadula* Zett. by most North American authors before the publication of Dorst's revision in 1937. Dorst showed that *Macrosteles* was the correct generic name and divided the genus into three: *Davisonia*, *Sonronius*, and *Macrosteles*. The first two were treated as subgenera by Oman (1949); this treatment is followed here. More recently, Ribaut (1948) described *Sagatus*, to include *punctifrons*; this also is treated here as a subgenus.

The most reliable specific characters in *Macrosteles* are usually visible in the aedoeagus, which always must be examined if definite identifications are required. The basic type of colour pattern of the head is useful in separating the species into groups, and occasionally provides specific characters. On a basis of this pattern the species fall into three groups, one including the species of the subgenera *Davisonia*, *Sonronius*, and *Sagatus* (Fig. 3), the second the *Macrosteles variata* complex and *M. lepida* (Fig. 4), and the third the remaining species (Fig. 5). The shape of the head is sometimes of specific significance. In all species the head tends to be relatively longer at the middle in the female than in the male. The shape of the seventh sternite of the female often serves to separate the species into groups, but, because of the variation that occurs, is not of specific significance in most instances. It is often impossible to separate the females of closely related species.

Some degree of individual, local, and geographical variation occurs in most species, and in some it is very extensive. It affects the size; the shapes of various parts of the body including the vertex, the seventh sternite of the female, and the aedoeagus; and the presence or absence, the size, and the intensity of the dark markings. In general, the males tend to be darker and more variable than the females.

Key to Subgenera and Species

1. Male pygofer with small digitate process on posterior margin (Fig. 8); mid line of face dark (Fig. 2), if pale then face either wholly pale or with other dark markings only feebly indicated; vertex typically with four pairs of spots, the median pair usually linear (Fig. 5) but if absent or rudimentary then the posterior pair either large (Fig. 4), or absent or rudimentary; vertex never with median spots large and rounded and remaining spots reduced or absent. (Subgenus *Macrosteles*) 8

   Male pygofer without digitate process on posterior margin; mid line of face pale, bordered at each side by a dark band (Fig. 1), or face wholly pale; vertex basically with five pairs of spots, the median pair large and rounded, the remainder reduced or absent (Fig. 3) 2

2. Male pygofer with weak notch in posterior margin (Fig. 7); front margin of head, viewed from above, evenly curved from middle to sides of eyes, the eyes not obviously protruding beyond the line of the vertex beside them; side margins of pronotum short; more slender species. (Subgenus *Sonronius*) 4

   Male pygofer without a notch in its posterior margin (Fig. 6); front margin of head, viewed from above, with the eyes distinctly protruding beyond the line of the vertex next the eyes; side margins of pronotum longer; more robust species 3

3. Fore wing wholly pale; apical processes of aedoeagus long, spine-like, pointing dorsally at right angles to the shaft. (Subgenus *Sagatus*) ..... 1. *punctifrons* (Fall.)

   Fore wing tinged brownish or with brownish streaks between the veins; apical processes of aedoeagus shorter, reflexed. (Subgenus *Davisonia*) 6

4. Fore wing with clavus and apical third brown, remainder yellow (Fig. 117) ..... 7. *clavata* (DeL. & D.)

Fore wing not as above 5
5. Veins of fore wing, at least in male, partly or wholly brown ..... 6. *quadripunctata* (Fall.)
Veins of fore wing wholly pale ..... 5. *arcuata* (G. & B.)
6. Pronotum with large, brown patch on disc at each side of mid line; scutellum with black basal triangles ..... 2. *americana* (Van D.)
Pronotum without such large brown patches; scutellum usually wholly pale, sometimes with brown basal triangles 7
7. Larger species, 5.0-7.0 mm. in length; fore wing more or less streaked brown between the veins; seventh sternite of female with a median, longitudinal, raised ridge ..... 3. *major* (Dorst)
Smaller species, 4.0–5.0 mm. in length; fore wing tinged fuscous between the veins; seventh sternite of female without a raised ridge ..... 4. *snowi* (Dorst)
8. Posterior spots of vertex large, rounded; median spots reduced and not linear, or, usually, absent (Fig. 4) 9
Posterior spots of vertex sometimes absent or very small, if moderate or large then median spots always present and linear in form (Fig. 5) 10
9. Apex of each apical process of aedoeagus with a triangular, flattened expansion having a serrated edge ..... 9. *lepida* (Van D.)
Apex of each apical process of aedoeagus simple, not expanded, flattened, or serrated ..... 8. *variata* (Fall.) complex
10. Apical processes of aedoeagus crossing each other 15
Apical processes of aedoeagus not crossing each other but diverging or parallel 11
11. Apical processes of aedoeagus each with two branches 22
Apical processes of aedoeagus not branched 12
12. Apical processes of aedoeagus forming a U in ventral view ..... 18. *curvata* n. sp.
Apical processes of aedoeagus not forming a U in ventral view, usually diverging 13
13. Apical processes of aedoeagus almost parallel in ventral view, very long, in lateral view strongly curved ..... 21. *laevis* (Rib.)
Apical processes of aedoeagus diverging in ventral view, shorter, in lateral view usually less strongly curved 14
14. Shaft of aedoeagus with longitudinal dorsal flange ..... 20. *cristata* (Rib.) complex
Shaft of aedoeagus without longitudinal dorsal flange ..... 19. *fascifrons* (Stål) complex
15. Apical processes of aedoeagus spine-like, curved downward near their bases to point anteriorly more or less parallel to the shaft or downward at right angles to the shaft 16
Apical processes of aedoeagus more or less flattened, not or only feebly directed downward, never pointing anteriorly 18
16. Apical processes of aedoeagus pointing downward at right angles to shaft; fore wing almost wholly uniformly blackish ..... 12. *osborni* (Dorst)
Apical processes pointing anteriorly, lying more or less parallel to the shaft; fore wing never almost uniformly blackish, usually more or less pale 17
17. Larger species, length 5.0–5.5 mm.; vertex twice as wide between the eyes as its median length ..... 10. *elongata* n. sp.
Smaller species, length 3.0–3.5 mm.; vertex less than twice as wide between the eyes as its median length ..... 11. *divisa* (Uhl.)
18. Smaller species, length 3.0 mm. or less 19
Larger species, length 3.5 mm. or more 21
19. Vertex pointed, one-fifth longer at middle than next the eye ..... 13. *potoria* (Ball)
Vertex rounded, hardly more than one-tenth longer at middle than next the eye 20
20. Apical processes of aedoeagus in line with shaft in lateral view ..... 14. *slossoni* (Van D.)
Aedoeagus curved upward at apex of shaft and downward at bases of processes in lateral view ..... 15. *skalkaensis* n. sp.
21. Apical processes of aedoeagus each with a flattened, rounded expansion near base in lateral view; vertex broadly rounded in front, at least two-sevenths longer at middle than next the eye ..... 16. *salina* (Reut.)
Apical processes of aedoeagus not expanded near their bases; vertex usually more or less pointed, less than two-sevenths longer at middle than next the eye ..... 17. *fieberi* (Edw.)
22. Apical processes of aedoeagus forming a U in ventral view with the apex of each arm branched into a short, blunt, laterally directed process and a long, slender, posteriorly directed spine; vertex largely black ..... 24. *borealis* (Dorst)
Aedoeagus not as above; vertex largely or wholly pale 23
23. Apical processes of aedoeagus long, stout, parallel, each branched into a straight spine in line with shaft and an outwardly directed, curved spine; dark markings of vertex well developed ..... 23. *bifurcata* n. sp.
Apical processes of aedoeagus slender, diverging, each branched into a slender, posteriorly directed spine and a short, slender internal spine, the latter often reduced

and sometimes represented only by an angle on the inner margin of the process; dark markings of vertex reduced or absent ..... 22. *obsoleta* (Dorst)

1. *Macrosteles* (*Sagatus*) *punctifrons* (Fall.)

Figs. 11, 35, 36, 76

Cicada punctifrons Fallen, 1826: 42.

Length 5.0–6.5 mm. General colour yellow, tinged greenish, with the large spots of the vertex black and the other dark markings of the body brown.

The seventh sternite of the female and the aedoeagus are distinctive. On external characters the species can be distinguished from *major* and *americana* by its less robust build and by the absence of dark markings on the fore wings; the latter character also distinguishes it from *snowi*. The species was formerly confused with *americana*, and American records for *punctifrons* var. *repleta* apparently refer to that species. *M. punctifrons* has been found in North America only in New York, and may be an artificial introduction. Specimens examined from:—Germany; Russia.

2. *Macrosteles* (*Davisonia*) *americana* (Van D.)

Figs. 10, 31, 32, 74, 114

Cicadula punctifrons var. *repleta* auctt. Amer. (nec. Fieber, 1885: 49).
Cicadula punctifrons var. *americana* Van Duzee, 1891: 169.
Davisonia delongi Dorst, 1937: 6.

A robust species, 4.5–5.0 mm. in length, tawny yellow with the large spots of the vertex and the basal angles of the scutellum black, other dark markings of the body brown, and the fore wings with broad, brown streaks between the veins.

The brown areas on the pronotum and the forms of the aedoeagus and the seventh sternite of the female are distinctive. These characters, together with its smaller size and shorter lateral margins of the pronotum, distinguish the species from *major*, which it resembles in shape of the head. It has been found on *Salix* spp., and appears to be widely distributed in the temperate parts of North America. Specimens examined from:—Canada: Ontario.

3. *Macrosteles* (*Davisonia*) *major* (Dorst)

Figs. 6, 9, 33, 34, 75, 115

Cicadula major Dorst, 1931: 43.

The largest and most robust species of the genus. Length 5.5–7.5 mm. Tawny yellow with the large spots of the vertex black, the other dark markings of the body brown, and with greyish or brown streaks between the veins and in the apical cells of the fore wing.

It is easily distinguished by its large size, by the aedoeagus, and by the seventh sternite of the female. It has been found on *Salix* spp., and appears to be widely distributed in the temperate parts of North America east of the Rocky Mountains. Specimens examined from:—Canada: Manitoba; United States: Colorado, Iowa, and Missouri.

4. *Macrosteles* (*Davisonia*) *snowi* (Dorst)

Figs. 12, 37, 38, 77

Cicadula snowi Dorst, 1931: 41.

Length 4.5–6.0 mm. General colour yellow, tinged greenish. The large spots of the vertex black, the other dark markings brown. The degree of development of the dark markings varies. Fore wings usually more or less streaked with brown between the veins.

The forms of the seventh sternite of the female and of the aedoeagus are distinctive. The species resembles *punctifrons* to some extent on external characters but can be distinguished by the genital characters and by the usual presence of brown streaks between the veins of the fore wings. It has been found on *Salix* spp. and has been recorded from localities in central and western

North America, but apparently not from the east. Specimens examined from:—Canada: Saskatchewan; United States: Colorado.

5. *Macrosteles* (*Sonronius*) *arcuata* (G. and B.)

Figs. 3, 13, 39-42, 78

Cicadula arcuata Gillette and Baker, 1895: 105.
?*Cicadula suffusa* Osborn, 1915: 146. New synonymy.

Length 4.0–5.0 mm. General colour greenish-yellow. The large spots of the vertex are black and the other dark markings, when present, brown. A form of the female found occasionally with the ordinary form has the vertex and face bright orange-red. This agrees with Osborn's description of *suffusa*, of which only females are known. Dorst (1937) stated that *suffusa* agrees exactly with the European species *binotata* Sahlberg (1871, p. 242), which also appears to be known only from the female. However, *arcuata* does not seem to have been found in Europe, perhaps indicating that *binotata* is a distinct species or a variety of another species, or that both *binotata* and *suffusa* are varieties of *quadripunctata* that lack the dark markings on the veins and thus cannot be distinguished from *arcuata*.

The species resembles *quadripunctata* but is distinguished by the form of the aedoeagus and by having the veins of the fore wings wholly yellow, not marked with brown as is usual in that species. However, the females of the two are sometimes difficult to separate. The species has a Boreal and mountain distribution. Specimens examined from:—Alaska; Canada: British Columbia, Manitoba, Ontario, Quebec, and Saskatchewan; United States: Colorado.

6. *Macrosteles* (*Sonronius*) *quadripunctata* (Fall.)

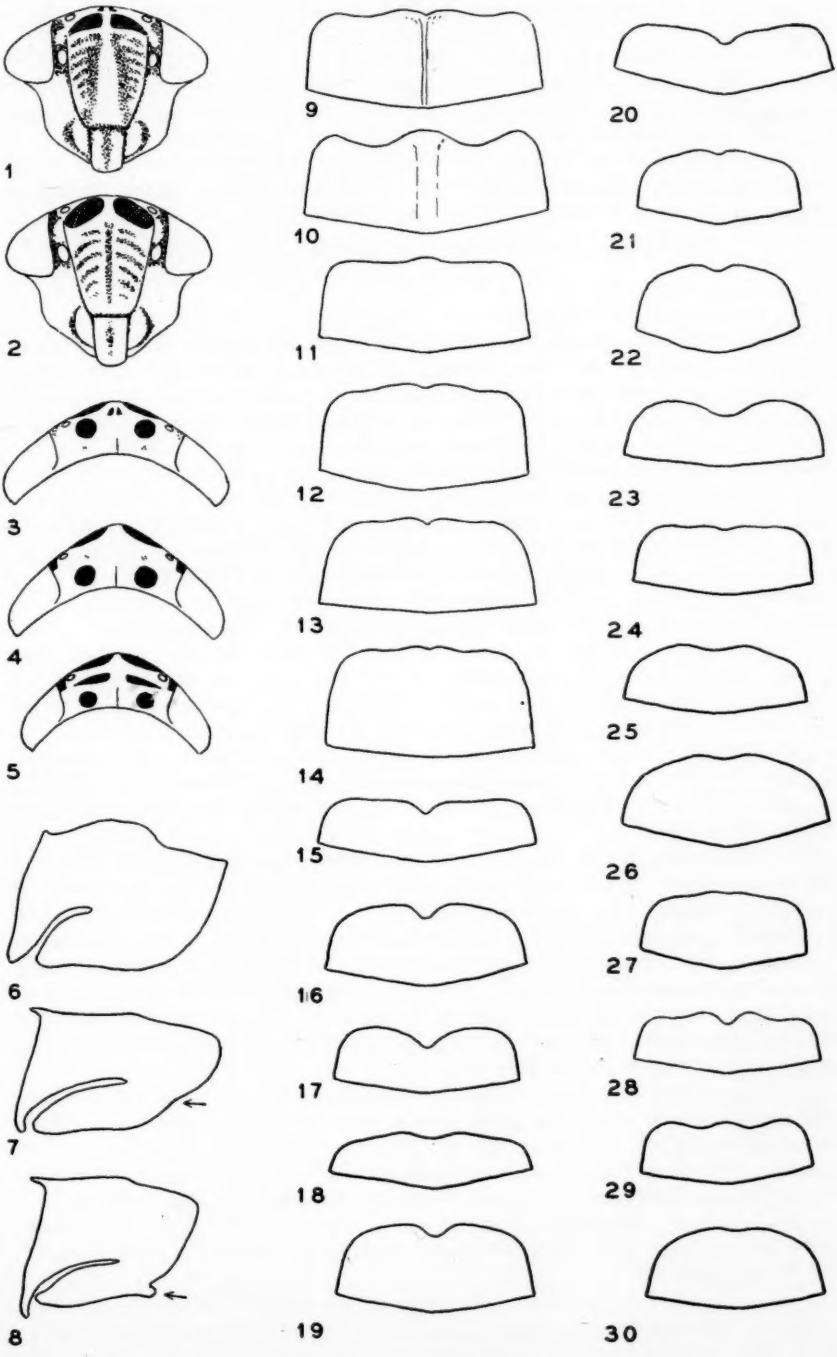
Figs. 1, 7, 14, 43-47, 79, 116

Cicada 4-punctata Fallen, 1806: 32.
Cicada maculipes Zetterstedt, 1840: 298.
Cicadula dahlbomi Zetterstedt, 1840: 298.
Jassus laetus Uhler, 1876: 360.
Cicadula warioni Lethierry, 1878: 127.
Eutettix vanduzeei Gillette and Baker, 1895: 103.
Cicadula ungae Ashmead, 1904: 134. New synonymy.

Length 4.0–6.0 mm. General colour tawny yellow. The dark markings of the body are black or dark brown and the veins of the fore wing usually are at least partly brown, but occasionally are wholly pale in the female. There is much individual variation in the extent of the dark markings. In general, males tend to be darker than females, and specimens from damp, northern localities tend to be darker than those from more southerly districts. The original description (Ashmead, 1904) and Dorst's (1937) figure indicate that *C. ungae* is a form with the dark markings well developed, as in Fig. 47.

The form of the aedoeagus is distinctive. This, and the brown markings on the veins, distinguish the species from *arcuata*. It has a wide distribution in the Boreal region and in the mountains of the west. Specimens examined from:—Alaska; Canada: Alberta, British Columbia, Labrador and Newfoundland, and Quebec; Germany; United States: Arizona, Colorado, New Mexico, Utah, and Wyoming.

Figs. 1-2. Face, showing colour pattern, of: 1, *Macrosteles quadripunctata*; 2, *M. sexnotata*.
Figs. 3-5. Vertex, showing basic colour pattern, of: 3, *M. arcuata*; 4, *M. variata*; 5, *M. fascifrons*.
Figs. 6-8. Male pygofer of: 6, *M. major*; 7, *M. quadripunctata*; 8, *M. sexnotata*.
Figs. 9-30. Female seventh sternite (in situ) of: 9, *M. major*; 10, *M. americana*; 11, *M. punctifrons*; 12, *M. snowi*; 13, *M. arcuata*; 14, *M. quadripunctata*; 15, 16, *M. variata*; 17, *M. lepida*; 18, *M. fascifrons*; 19, *M. elongata*; 20, *M. potoria*; 21, *M. slossoni*; 22, *M. skalkabiensis*; 23, *M. salina*; 24-26, *M. fascifrons*; 27, *M. cristata*; 28, *M. laevis*; 29, *M. obsoleta*; 30, *M. borealis*.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7. *Macrosteles* (*Sonronius*) *clavata* (DeL. & D.)

Figs. 48, 80, 117

Cicadula clavata DeLong and Davidson, 1934: 223.

Length 4 mm. A bright yellow species with black markings on the body and with the fore wing dark smoky or brown on the clavus and on the apical third.

The colour of the fore wing and the form of the aedoeagus are distinctive. The vertex is relatively longer at the middle than those of the two other species of the subgenus. The species has been found only in New Jersey. Specimen (paratype) examined from:—United States: New Jersey.

8. *Macrosteles* (*Macrosteles*) *variata* (Fall.) complex

Figs. 4, 15, 16, 49-56, 81, 82, 118

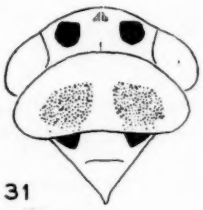
Cicada variata Fallen, 1806: 34.
Jassus fumatus Herrich-Schaeffer, 1838: 5.

This may be a complex of several species that are poorly defined morphologically. Length 3.5–4.5 mm. General colour tawny yellow, yellow, or greenish-yellow, the body with black or dark-brown markings, and the fore wing usually with yellowish-brown or brown streaks between the veins, the streaks forming irregular, oblique, transverse bands on the wings. There is local and individual variation similar to that of the *fascifrons* complex except in extent. The common form has the vertex marked as in Fig. 49, and the fore wing as in Fig. 118, but there is much individual variation in size, in size of the markings, in the relative lengths of the apical processes and lateral teeth of the aedoeagus (Figs. 81, 82), in the shape of the seventh sternite of the female (Figs. 15, 16), and to some extent in the shape of the vertex. A form that occurs with the ordinary form in some localities and largely replaces it in others tends to have the vertex more rounded in front, the posterior spots smaller, the pronotum usually black or dark brown except on the mid line and broadly along the posterior margin (Figs. 54, 55), and the fore wing brownish or blackish except broadly along the costa. It intergrades with the ordinary form. Another form, which apparently replaces the ordinary form in some localities, has the vertex slightly shorter and more rounded and is tawny yellow without dark markings, except the anterior and posterior spots of the vertex and the basal triangles of the scutellum (Fig. 56).

This complex and *M. lepida* differ from other species of the genus in having the posterior spots of the vertex large and rounded and the median spots reduced or, usually, absent. The two often are difficult to separate on external characters but can be distinguished readily by the aedoeagus: in *lepida* each apical process is expanded and flattened at its tip whereas in the *variata* complex each apical process tapers smoothly to a point; moreover, in the *variata* complex the processes usually, but not always, extend anteriorly more or less parallel with the shaft whereas in *lepida* they diverge laterally. In *lepida* there are never dark markings in the form of bands on the fore wing.

This complex has a wide range in North America and is often common, especially in damp situations. The insects have been found on sugar beet in Iowa (Jones, 1929) and on carrot in Alberta. Specimens examined from:—Canada: Alberta, British Columbia, Manitoba, Ontario, and Quebec; Germany; United States: California, Colorado, Connecticut, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, New Hampshire, New York, Ohio, Tennessee, Utah, Virginia, and Washington.

Figs. 31-48. Head, pronotum, and scutellum of: 31, 32, *Macrosteles americana*; 33, 34, *M. major*; 35, 36, *M. punctifrons*; 37, 38, *M. snowi*; 39-42, *M. arcuata*; 43-47, *M. quadripunctata*; 48, *M. clavata*. (Drawings to same scale)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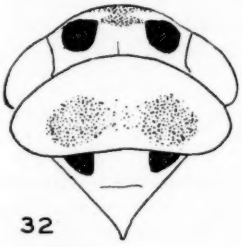
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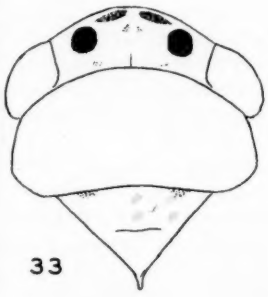
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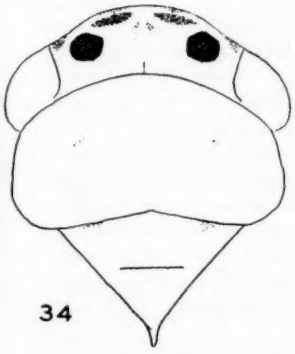
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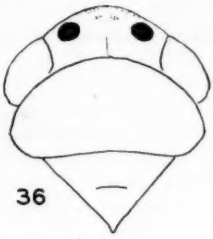
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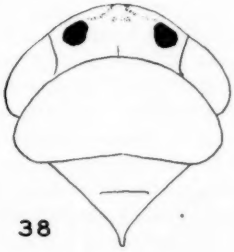
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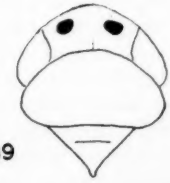
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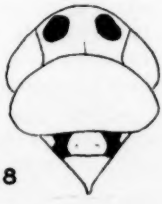
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9. *Macrosteles* (*Macrosteles*) *lepida* (Van D.)

Figs. 17, 57, 58, 83

Cicadula lepida Van Duzee, 1894: 139.

Length 3.2–4.0 mm. General colour yellow, sometimes tinged greenish, with the spots of the vertex and of the scutellum black and the fore wing tinged smoky between the veins at its base or throughout.

The flattened and expanded apices of the apical processes of the aedoeagus are distinctive. Externally, the species is difficult to separate from forms of the *variata* complex that lack dark markings on the fore wings. It has a wide range in eastern United States but appears to be rather local in its distribution. Specimens examined from:—United States: Iowa, Maryland, Massachusetts, New York, Pennsylvania, Tennessee, and Virginia.

10. *Macrosteles* (*Macrosteles*) *elongata* n. sp.

Figs. 19, 59-62, 84

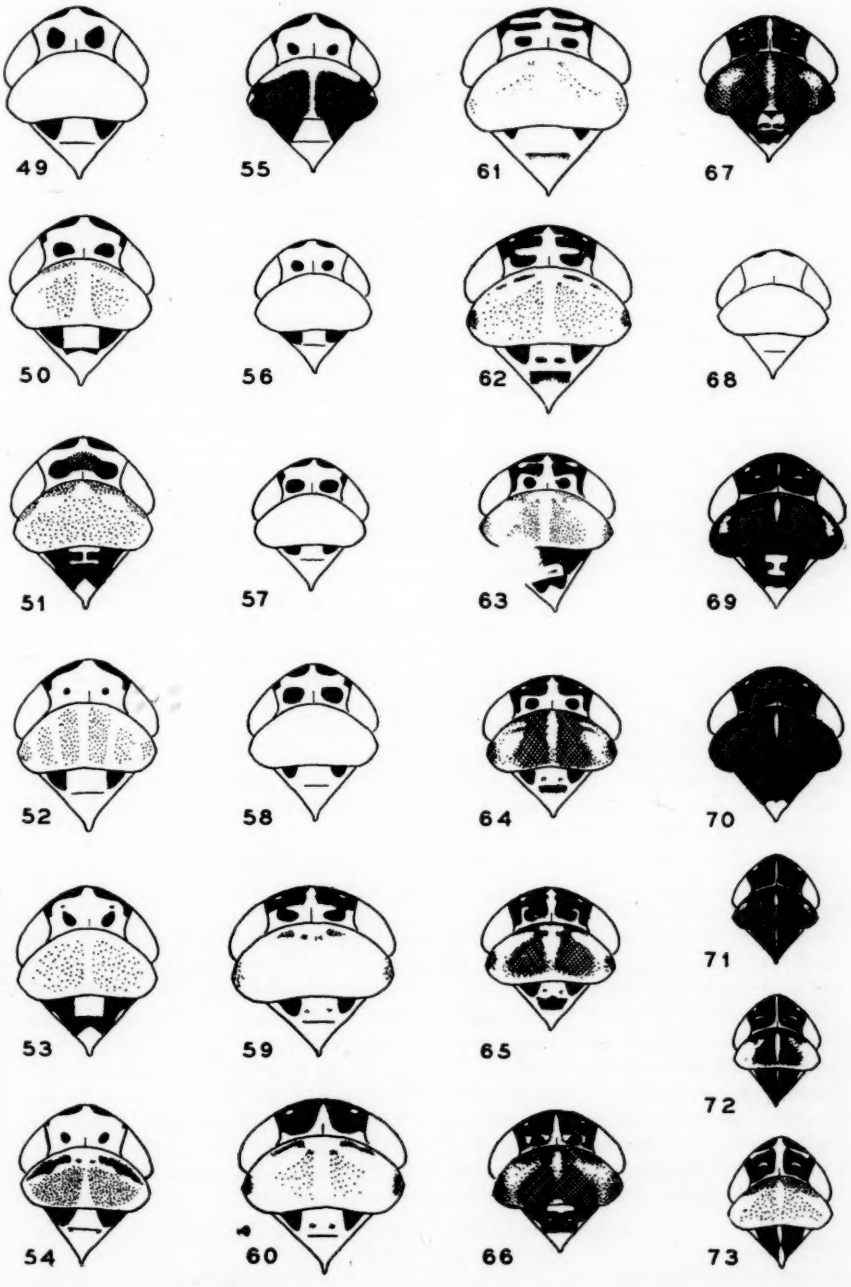
?*Macrosteles fascifrons* Medler, 1942: 119 (nec Stål, 1858: 194).

Length 5.0–5.5 mm. Vertex rounded in front, in female one-twelfth longer at middle than next the eye, in male hardly longer at middle than next the eye. Fore wing one-quarter longer than the abdomen in the female, one-third longer in the male. Aedoeagus in lateral view with shaft feebly curved, in ventral view tapered slightly toward base, with two spine-like, curved apical processes that cross each other near their bases and curve downward and anteriorly to lie more or less parallel to the shaft on its ventral side, pointing anteriorly and extending to more than half the length of shaft; shaft with a short ventro-lateral tooth at each side of apex. Seventh sternite of female with a wide, shallow, V-shaped emargination in the middle of its posterior margin.

General colour greenish-yellow, with heavy black markings. Vertex with posterior spots black, ovoid, wider than long; anterior spots black, confluent laterally with the lateral spots; median spots black, broad, linear, confluent laterally with the lateral spots; anterior and median spots frequently enlarged and confluent, posterior and median spots occasionally confluent, and vertex sometimes wholly black except at the ocelli, the median line, and the posterior margin. Face with median stripe, lateral arcs, and sutures black, the dark markings often enlarged and confluent. Pronotum with brownish or blackish markings near anterior margin and at side margins, in dark specimens frequently suffused brown or greenish-brown on disc at either side of mid line. Scutellum with black basal triangles, and usually with the transverse impression brown and with a pair of dark spots on disc. Thorax variously marked brownish or blackish beneath. Abdomen suffused brownish or black ventrally in middle of anterior segments, black dorsally except the lateral and posterior margins of the segments. Femora longitudinally striped brownish or black; tarsi darkened apically. Fore wing hyaline whitish-yellow, tinged greenish, frequently smoky between the veins; in dark specimens with a smoky suffusion in basal half and at apex of clavus, along the claval suture, and in the apical cells, and forming irregular transverse bands before and beyond middle; commissure frequently dark brown at basal half and at apex of clavus.

This distinctive species resembles the *variata* complex and *divisa* in the form of the aedoeagus. It is easily separated from the latter species by its much larger size and its short, wide, rounded vertex. These characters, and also the colour pattern of the vertex, separate it from the *variata* complex. This species appears to agree with Medler's (1942) description of "*fascifrons*" from Minnesota. Described from 12 specimens collected in the Cariboo district of British Columbia.

Holotype—♂, Quesnel, British Columbia, July 24, 1949 (R. Stace-Smith). No. 5972 in the Canadian National Collection, Ottawa.



Figs. 49-73. Head, pronotum, and scutellum of: 49-56, *Macrosteles variata* complex; 57, 58, *M. lepida*; 59-62, *M. elongata*; 63-68, *M. divisa*; 69, 70, *M. osborni*; 71-73, *M. potoria*. (Drawings to same scale)

Allotype—♀, same data as holotype.

Paratypes—4 ♂, 5 ♀, same data as holotype. 1 ♀, on grasses, Macalister, British Columbia, July 29, 1949 (R. Stace-Smith).

Holotype, allotype, and paratypes in the Canadian National Collection, Ottawa.

11. *Macrosteles* (*Macrosteles*) *divisa* (Uhl.)

Figs. 63-68, 85, 119

Cicadula divisa Uhler, 1877: 472.

?*Macrosteles fascifrons* Dorst, 1937: 15 (nec Stål, 1858: 194).

Length 3.0–3.5 mm. General colour yellow, tinged greenish, heavily marked with black. There is much variation, both local and individual. The black markings are often enlarged and more or less confluent; sometimes the vertex is wholly black except at the ocelli and the mid line and along the posterior margin; and the face, pronotum, and scutellum are largely black. Rarely, the dark markings are reduced or absent. The fore wing is usually brownish to dark blackish-brown, becoming paler toward apex, where the crossveins are sometimes whitish, and having whitish hyaline spots near its base and at middle and on the commissure at middle of clavus.

This is not the species that has been referred to by most North American authors as *Cicadula divisa* or *Macrosteles divisa*, and formerly as *Cicadula sexnotata*. That species—the six-spotted leafhopper—is the *M. fascifrons* complex, which often resembles *divisa* externally but has very different male genitalia. I have been unable to find reliable morphological characters for separating the females of the two. A co-type of *divisa* from Uhler's series in the United States National Museum is shown in Fig. 63; this specimen has been selected as lectotype. The characteristics of the species are that it resembles a dark form of the *fascifrons* complex on external characters whereas the aedoeagus resembles that of the *variata* complex. The species is easily distinguished from the *variata* complex by the shape and the type of colour-pattern of the vertex. *M. elongata*, which it also resembles in genitalic characters, is a much larger insect with a differently shaped vertex. The species appears to have a wide but local distribution. Specimens examined from:—Canada: Saskatchewan; United States: Colorado, New York, Nevada, Utah, and Wisconsin.

12. *Macrosteles* (*Macrosteles*) *osborni* (Dorst)

Figs. 69, 70, 86, 120

Cicadula osborni Dorst, 1931: 45.

Length 4.0–5.0 mm. The darkest species of the genus; it is almost wholly black, including the fore wings. The female has not been recognized, and probably resembles forms of the female of other species found in the same area.

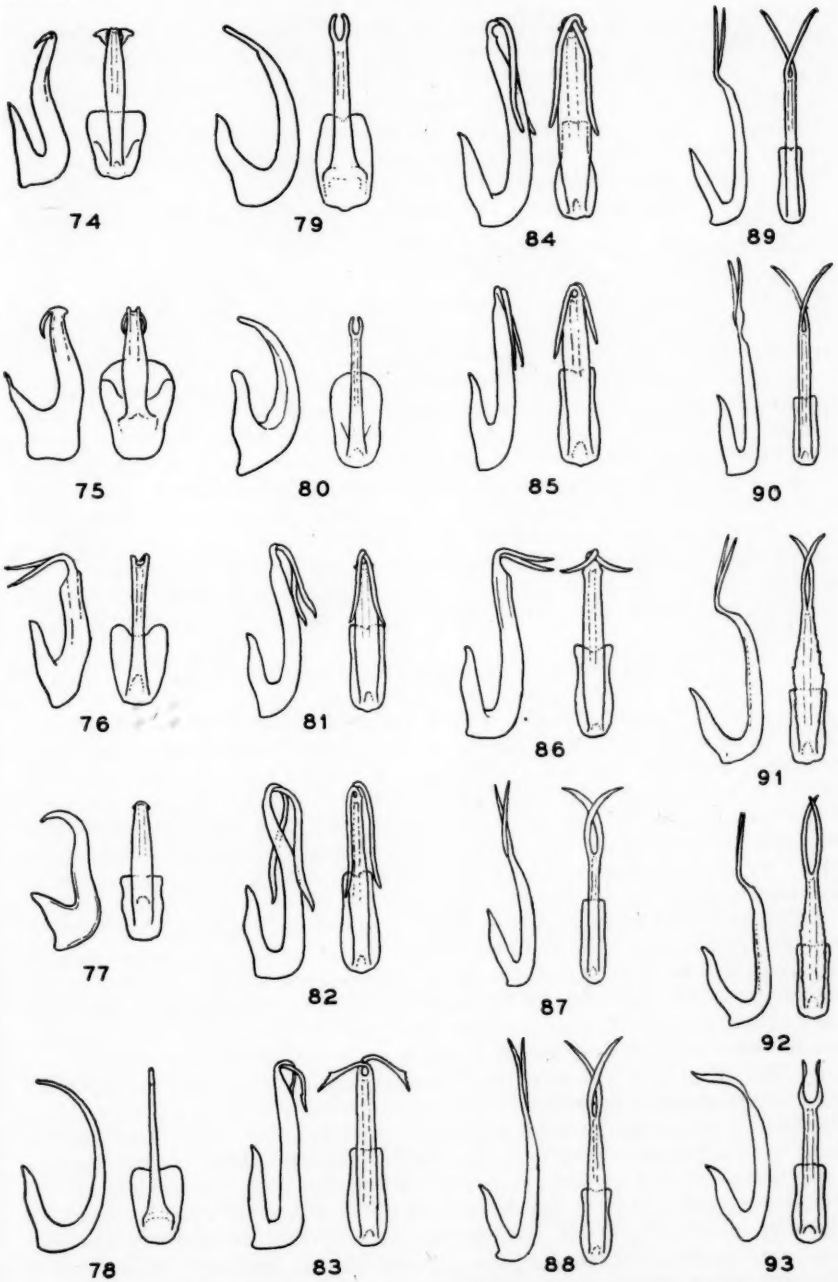
The almost uniform black colour is distinctive: dark specimens of other species tend to be less uniformly marked, particularly on the fore wing. Such specimens are easily distinguished by the form of the aedoeagus. In general form the aedoeagus resembles those of the *variata* complex, *divisa*, and *elongata*, but the apical processes are shorter and more nearly straight and point at right angles to the shaft. The species has been found only in Alaska, where it seems to have a wide distribution and appears to have been captured mainly in coastal marshes and at lake margins. Specimens examined from:—Alaska.

13. *Macrosteles* (*Macrosteles*) *potoria* (Ball)

Figs. 20, 71-73, 87

Cicadula potoria Ball, 1900: 346.

Length 2.0–2.5 mm. General colour pale yellowish with dark markings that usually are enlarged and confluent so that it appears largely blackish. The fore wing hyaline, more or less tinged smoky at base, and brownish on the commissure on the basal half and at the apex of the clavus.



Figs. 74-93. Lateral and ventral views of aedoeagus of: 74, *Macrosteles americana*; 75, *M. major*; 76, *M. punctifrons*; 77, *M. snowi*; 78, *M. arcuata*; 79, *M. quadripunctata*; 80, *M. clavata*; 81, 82, *M. variata* complex; 83, *M. lepida*; 84, *M. elongata*; 85, *M. divisa*; 86, *M. osborni*; 87, *M. potoria*; 88, *M. slossoni*; 89, *M. skalkahiensis*; 90, *M. salina*; 91, 92, *M. fieberi*; 93, *M. curvata*.

The species is easily distinguished by its small size and long, pointed vertex. The latter character separates it from *slossoni* and *skalkahiensis*, which are equally small in size and which resemble *potoria* in form of the aedoeagus. The form of the aedoeagus and the shape of the vertex distinguish it from small forms of the *fascifrons* complex. The species appears to have a wide but local distribution in eastern North America. Specimens examined from:—Canada: Manitoba; United States: Maine, New York, and Pennsylvania.

14. *Macrosteles* (*Macrosteles*) *slossoni* (Van D.)

Figs. 21, 88, 94-98, 121

Cicadula slossoni Van Duzee, 1893: 281.

Length 2.5–3.0 mm. General colour yellow tinged greenish, with heavy black markings that usually are confluent on the vertex. The fore wing is tinged with yellowish-brown or has brown streaks between the veins, the streaks forming oblique, irregular, transverse bands.

It can be distinguished from *potoria* by the shape of the vertex, from *skalkahiensis* by the form of the aedoeagus in lateral view and by the usually smaller size and darker markings, and from small forms of the *fascifrons* complex by the aedoeagus. Some forms of the *fascifrons* complex have the dark markings of the vertex confluent, forming a pattern similar to that of *slossoni*. Such forms were referred to as *slossoni* by Dorst (1937) and DeLong (1942). They differ from *slossoni* in their much larger size and in the aedoeagus. The species is widely distributed in eastern North America and appears to occur most commonly in damp places. Specimens examined from:—Canada: Nova Scotia and Ontario; United States: Maine, New Jersey, New York, Pennsylvania, Vermont, Virginia, and Wisconsin.

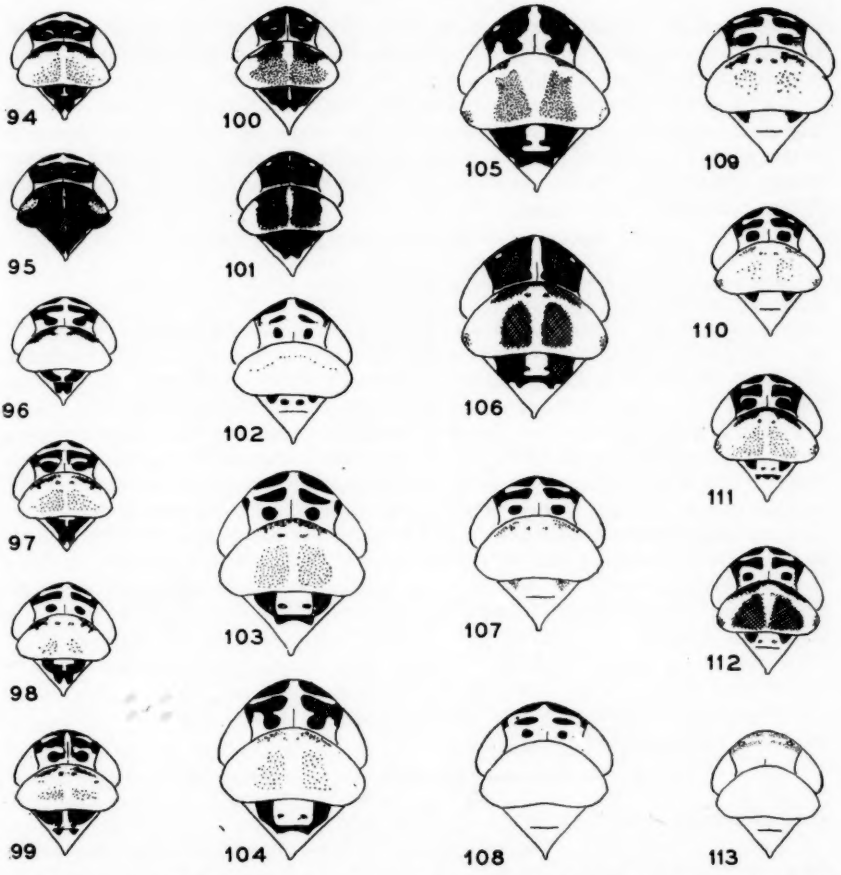
15. *Macrosteles* (*Macrosteles*) *skalkahiensis* n. sp.

Figs. 22, 89, 99-102, 122

Length 2.8–3.0 mm. Vertex in male rounded in front, fully one-tenth longer at middle than next the eye; in female obtusely pointed in front, one-sixth longer at middle than next the eye. Aedoeagus in lateral view with shaft distinctly curved upward at apex and apical processes curved downward near their bases, so that the latter extend parallel to the shaft but at a higher level; in ventral view the processes crossing one another near their bases and extending straight thereafter. Seventh sternite of female with a small, shallow median notch in its posterior margin.

General colour greenish-yellow, with well-developed black markings. Markings of vertex usually more or less confluent in male, the darkest specimens with the vertex wholly black except the ocelli, the posterior margin, and part of the median line. Face black except the lateral areas of the clypeus and a transverse band below the ocelli. Pronotum in male with dark markings near anterior margin and a brownish suffusion on disc at each side of mid line; wholly pale in female. Scutellum with black basal triangles and a pair of black median dots; in the male the markings enlarged and confluent with each other and with a dark suffusion on the transverse impression, the scutellum being wholly black except at the apex and sides in very dark specimens. Thorax beneath largely black in male, partly suffused blackish in female. Abdomen black dorsally except the posterior segments and the lateral margins of all segments; black ventrally in middle of anterior segments. Femora variously suffused brownish or blackish. Fore wing hyaline with an irregular, oblique, brown, transverse fascia, broken on suture before middle, and another beyond middle; apex of clavus brownish, and a brown suffusion in apical cells.

This species resembles *slossoni* in size but is easily distinguished by the form of the aedoeagus: in lateral view there is a double bend in the aedoeagus of



Figs. 94-113. Head, pronotum, and scutellum of: 94-98, *Macrosteles slossoni*; 99-102, *M. skalkahiensis*; 103-106, *M. salina*; 107-109, *M. fieberi*; 110-113, *M. curvata*. (Drawings to same scale)

skalkahiensis, whereas in *slossoni* the apical processes extend in line with the shaft. Moreover, in *slossoni* the median spots of the vertex apparently never are confluent with the anterior spots, whereas in *skalkahiensis* they frequently are confluent medially.

Holotype— ♂, Skalkaho Pass, Ham. [Hammond?], Montana, August 1, 1949 (R. H. Beamer).

Allotype— ♀, same data as holotype.

Paratypes—4 ♂, same data as holotype.

Holotype, allotype, and paratypes in the Snow Entomological Museum, University of Kansas; paratypes in the Canadian National Collection, Ottawa.

16. *Macrosteles* (*Macrosteles*) *salina* (Reut.)

Figs. 23, 90, 103-106

Cicadula sexnotata var. *salina* Reuter, 1886: 211.

Length 3.5–4.0 mm. General colour greenish-yellow, with heavy black markings. The dark markings are usually distinct in the female but enlarged

and more or less confluent in the male. Fore wing yellowish-green, usually more or less tinged smoky throughout, with the commissure and the claval suture brown, the latter pale at middle.

This species has not been recorded previously for North America. Distinctive features are the long, rounded vertex of the female and the flattened expansion at the base of each apical process of the aedoeagus. Specimens examined from:—Alaska (Anchorage, Matanuska, Saldovia, Steese Highway, and Willow); Canada: British Columbia (Lake Atlin).

17. *Macrosteles* (*Macrosteles*) *fieberi* (Edw.)

Figs. 91, 92, 107-109

Cicadula frontalis Fieber, 1885: 45 (nec Scott, 1875: 231)
Cicadula fieberi Edwards, 1891: 32.
Macrosteles sexnotata Dorst, 1937: 16. (nec Fallen, 1806: 34). New synonymy.

Length 3.5–4.0 mm. General colour greenish-yellow with black markings. Markings of vertex usually isolated, occasionally barely confluent. Fore wings dull greenish-yellow, sometimes tinged brownish between the veins.

This European species has not been recorded previously for North America. On the basis of his figures, Dorst (1937) apparently mistook European specimens for *M. sexnotata* (Fall.). *M. fieberi* resembles closely the *fascifrons* complex and *curvata* in external appearance, and reliable characters for separating the females of the three have not been found. The form of the aedoeagus is distinctive. In lateral view it resembles that of *skalkabiensis* and to some degree that of *salina*, but the broader shaft in ventral view and the curved apical processes are distinctive. There appears to be some local variation in that the shaft of the aedoeagus is rather less curved and the fore wings tend to be more intensely tinged brownish in specimens from Quebec than in specimens from Alaska. The species has a Boreal distribution. Specimens examined from:—Alaska (Anchorage and Matanuska); Canada: Quebec (Natashquan) and Yukon Territory (M.P. 1221 on Alcan Highway); Germany.

18. *Macrosteles* (*Macrosteles*) *curvata* n. sp.

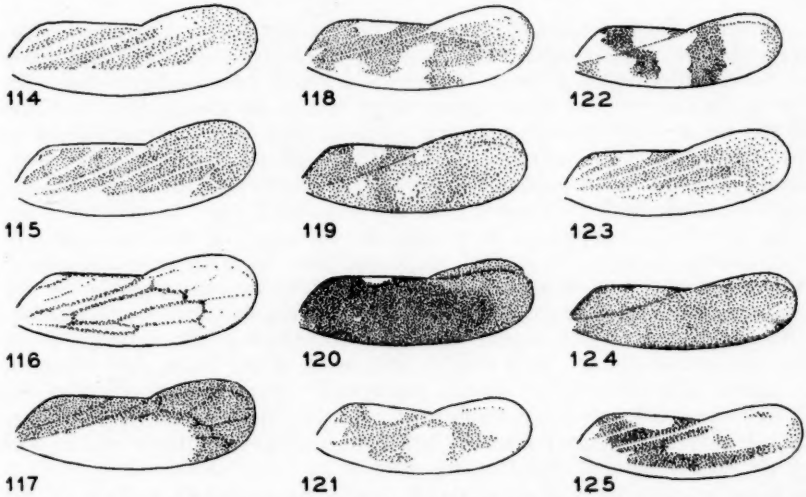
Figs. 93, 110-113

Macrosteles viridigriseus Dorst, 1937: 19 (nec Edwards, 1924: 54).

Length 3.0–3.5 mm. Vertex rounded in front, one-tenth longer at middle than next the eye. Aedoeagus with apical processes forming a U in ventral view, in lateral view curved upward to point at right angles to the shaft, each flattened throughout its length and twisted where it curves upward so that it is dorso-ventrally flattened at its base and laterally flattened on its apical two-thirds.

General colour greenish-yellow with black and brownish markings; dark markings occasionally absent or only feebly indicated. Markings of vertex isolated except that the median and lateral spots are usually confluent. Pronotum with dark-brown or blackish markings near anterior margin, and usually with a brownish suffusion on disc at either side of mid line. Scutellum with black basal triangles. Abdomen marked blackish. Fore wing dull yellowish-green, often faintly tinged smoky, with brownish markings on the commissure at basal half and at apex of clavus.

The form of the aedoeagus is distinctive and serves to distinguish the species from the *fascifrons* complex and *fieberi*, with which it often occurs. The three species cannot be separated reliably on external characters and no reliable characters for separating the females could be found. This is the species that Dorst (1937) discussed as *viridigriseus* (Edw.), and the description and figures in the present paper were made from specimens examined by Dorst. For example, the specimen shown in Fig. 113 is apparently that shown by Dorst, Fig. 5 U. The females described by Dorst apparently are a mixture of this species, the *fascifrons*



Figs. 114-125. Left fore wing of: 114, *M. americana*; 115, *M. major*; 116, *M. quadripunctata*; 117, *M. clavata*; 118, *M. variata* complex; 119, *M. divisa*; 120, *M. osborni*; 121, *M. slossoni*; 122, *M. skalkahiensis*; 123, 124, *M. fascifrons* complex; 125, *M. borealis*.

complex, and *fieberi*. *M. viridigriseus*, of which I have examined a paratype and a number of other specimens from England and Germany, differs in the form of the aedoeagus: in ventral view there is a serrated flange on each side of the shaft, and the apical processes, though forming a U, are not flattened and do not curve upward. North American records for *viridigriseus* are therefore incorrect. Described from 19 males collected in Labrador and northeastern Quebec.

Holotype—♂, Bradore Bay, Quebec, August 2, 1930 (W. J. Brown). No. 5973 in the Canadian National Collection, Ottawa.

Paratypes—♂, Bradore Bay, Quebec, August 2, 1930 (W. J. Brown), August 9, 1930 (W. J. Brown) (two specimens), August 4, 1940 (W. J. Brown), and July 27, 1929 (W. J. Brown); Natashquan, Quebec, August 7, 1929 (W. J. Brown); Hopedale, Labrador, August 9, 1926 (W. W. Perrett) (eight specimens) and August 5, 1931 (W. W. Perrett); and N.W. River, Labrador, July, 1935 (F. C. Sears) (three specimens).

Holotype and paratypes in the Canadian National Collection, Ottawa; paratypes in the United States National Museum, Washington, D.C.

19. *Macrosteles* (*Macrosteles*) *fascifrons* (Stal) complex

Figs. 5, 18, 24-26, 123, 126-139, 151-187

Thamnotettix fascifrons Stål, 1858: 194.
Cicadula sexnotata auctt. Amer. (nec Fallen, 1806: 34).
Cicadula divisa auctt. Amer. (nec Uhler, 1877: 472).
Cicadula quadrilineata Forbes, 1885: 68.
Cicadula pallida Osborn, 1915: 146.
Cicadula scripta DeLong, 1924: 67.
Macrosteles slossoni Dorst, 1937: 18 (nec Van Duzee, 1893: 281).
Macrosteles wilburi Dorst, 1937: 19.

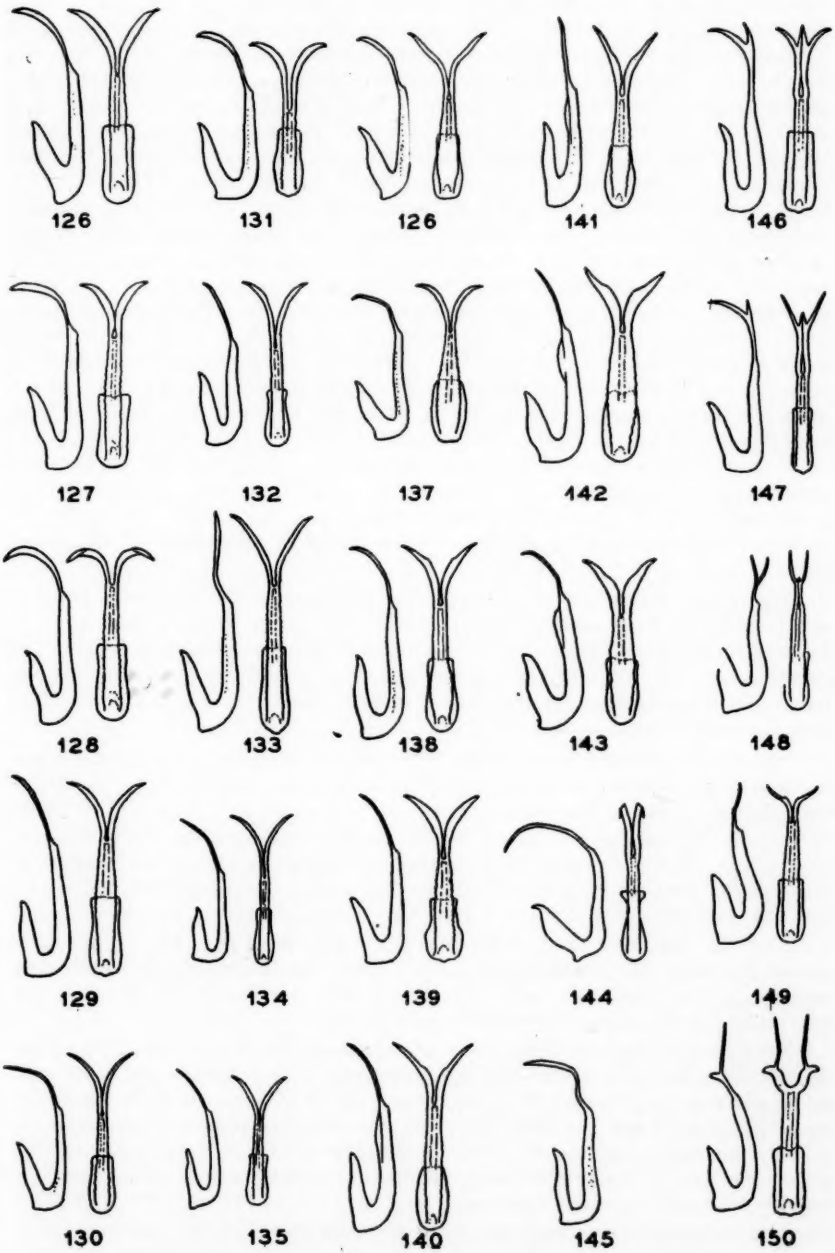
This complex consists of a number of local or geographical forms in each of which there is individual variation, often extensive. This variation is such that the forms intergrade in morphological characters. Because constant morphological characters for separating them were not found, the status of these forms is not clear. Biological data and breeding experiments may be necessary to demonstrate their status.

It is possible that some of the forms may be physiological species that are poorly defined morphologically. The wide range of the complex as a whole and the apparent habitat differences between different forms indicate this. The range of the complex as a whole extends from Mexico and Puerto Rico to Alaska and the borders of the Arctic tundra. The habitats include grasslands of all types from sea-level to altitudes of over 9,500 feet and from swamps to dry prairies. Severin (1940) stated, without giving details, that the form found in the Montera Mountains, California, will not interbreed with the common form of the eastern United States. It is possible that some of the forms may be environmental varieties. In general, specimens from damp localities and regions tend to be relatively dark in general hue and to have the dark markings of the body enlarged and confluent, whereas specimens from dry and warm situations or regions tend to be pale in general hue and to have the dark markings of the body reduced or absent. It is possible that some of the forms may represent populations that are or were isolated ecologically from other populations and that developed independently during their isolation, though not to the species level. It may be significant that the largest number of local forms are in ecologically diverse regions, as in the mountains of the west. Moreover, the habits appear to be relatively sedentary, which would favour isolation: Linn (1940) found that the common form of the eastern United States did not spread in perceptible numbers more than 200 feet in four weeks.

The general features of the complex are: length 2.0–5.1 mm., usually 3.5–4.2 mm.; general colour usually yellowish-green, but varying from pale ochreous to greenish-fuscous, with the dark markings of the body black or brownish; fore wing usually hyaline, tinged yellowish-green, frequently tinged smoky between the veins near the commissure in the basal half and at the apex of the clavus, sometimes tinged fuscous between the veins throughout except broadly along the costa (Fig. 123), sometimes largely fuscous (Fig. 124), and sometimes clear hyaline. The distinctive feature of the complex as a whole is the form of the aedoeagus (Figs. 126-139). The aedoeagus resembles those of the *cristata* complex and *laevis* in general structure, but in the *cristata* complex there is a dorsal flange on the shaft, which is absent in the *fascifrons* complex, and *laevis* has the apical processes relatively long, strongly curved, and hardly diverging, whereas they always diverge moderately or strongly in the *fascifrons* complex. No reliable characters were found for separating females of the *fascifrons* complex from those of *divisa*, *fieberi*, *curvata*, or the *cristata* complex.

Most of the forms of the complex, other than those that are very small in size or that have the dark markings of the body either enlarged and confluent or absent or rudimentary, were known collectively as *Cicadula sexnotata* before 1937, and subsequently as *Macrosteles divisa*. The common name for these forms collectively is the six-spotted leafhopper. *Macrosteles sexnotata* is a European species that differs constantly from American forms in having a triple bend in the aedoeagus in lateral view (Fig. 145). Oman (1949) listed *sexnotata* as occurring in northeastern North America. It seems likely that this record may have been based on specimens of *fieberi* misidentified as *sexnotata* from Dorst's (1937) figure. As shown previously, the species described by Uhler as *divisa* is not the *divisa* of subsequent authors.

The dominant form in most parts of North America east of the Rocky Mountains apparently was that described by Forbes (1885) as *quadrilineata*. The genitalia are shown in Figs. 24-26 and 126-128. Normally the dark markings of the head are moderately developed (Figs. 169 and 170) and the fore wings are hyaline yellowish-green, frequently tinged smoky between the veins. Sometimes



Figs. 126-150. Lateral and ventral views of aedoeagus of: 126-139, *Macrosteles fascifrons* complex; 140-143, *M. cristata* complex; 144, *M. laevis*; 145, *M. sexnotata* (lateral view only); 146, 147, *M. bifurcata*; 148, 159, *M. obsoleta*; 150, *M. borealis*.

the dark markings are enlarged and confluent (Figs. 182, 183, and 185). Such forms occur both with the normal form and as more or less pure populations. They appear most frequent in damp regions or localities. Dorst (1937), followed by DeLong (1942), mistook a form that has the dark markings of the vertex similar to those of *slossoni* for that species. Examples of this form, which is easily distinguished from *slossoni* by its larger size and by the male genitalia, are shown in Figs. 182 and 183. Sometimes, particularly in warm, dry regions, the dark markings are reduced in size and any of them may be absent (Figs. 157, 159, 161). Occasionally the vertex is without dark markings. This type of variation occurs in other forms of the *fascifrons* complex (see below) and in other species of *Macrosteles*, namely, the *variata* complex, *divisa*, *curvata*, and the *cristata* complex. Two forms that lack dark markings on the vertex have been described as species, *pallida* and *wilburi*. The former was described from specimens collected by Osborn in Maine. A specimen from the Osborn Collection collected in Maine is shown in Figs. 130 and 154. *M. wilburi* was described from specimens collected in a locality in Kansas, where it apparently occurred as a more or less pure population, though one paratype examined had the four pairs of dark markings present on the vertex. Paratypes are shown in Figs. 134 and 153. The characters given by Dorst (1937) to distinguish *pallida* from *wilburi* do not hold good, because of individual variation. No reliable morphological characters could be found for separating these forms from each other and from the unmarked or weakly marked specimens often found in populations of the normal form.

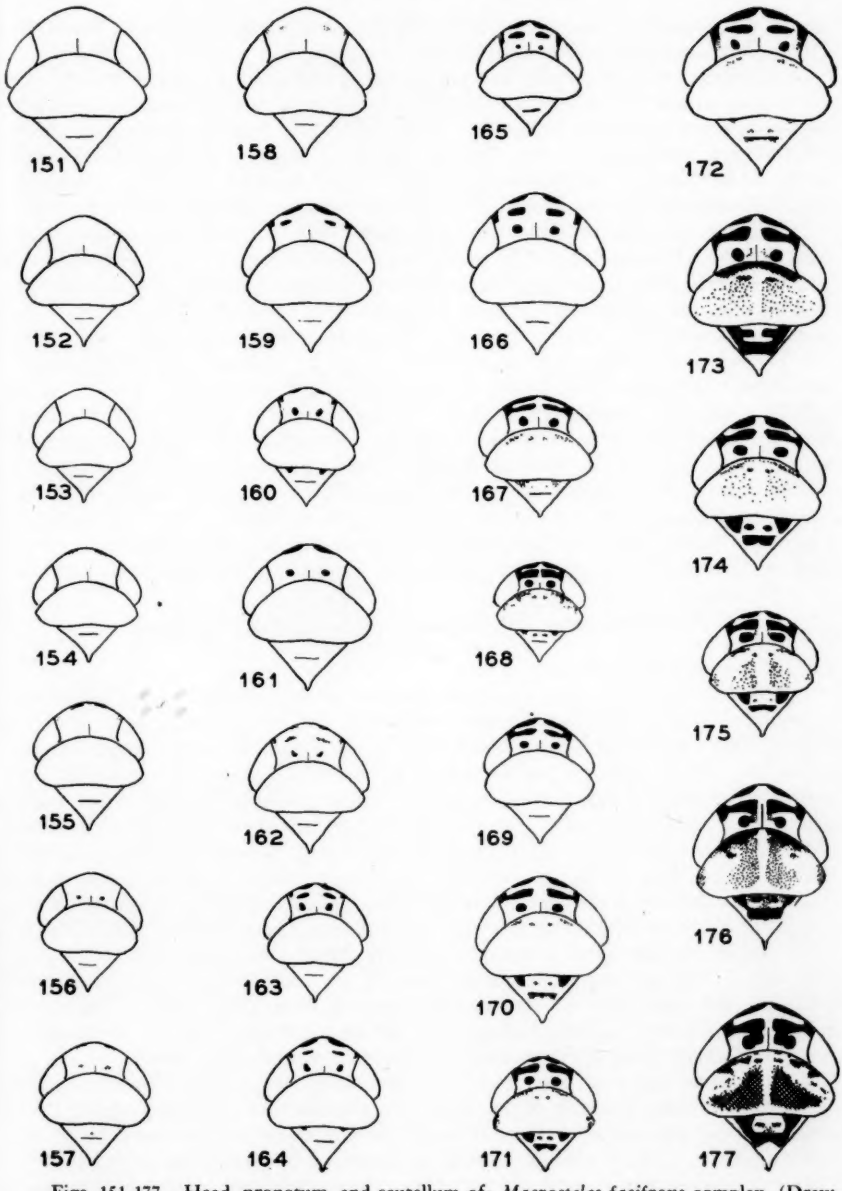
In swamps in Florida and Georgia the predominant form is very small in size, averaging 2.0–2.5 mm. in length, and has the vertex rounded in front with the dark markings moderately developed. Specimens from the type locality are shown in Figs. 135, 167, and 168. It was described by DeLong as *scripta*. Though apparently forming pure populations in some localities, in others it intergrades with the normal form in size.

Specimens examined from Puerto Rico had the vertex rounded in front and relatively narrow between the eyes and the fore wings clear hyaline. A similar form occurs locally in Texas.

In and west of the Cordilleras and in parts of the Boreal region the insects tend to have the vertex relatively long and pointed. The holotype of *fascifrons* (Figs. 18 and 176) is typical of this form; other specimens are shown in Figs. 136, 138, 139, 174, 175, 177, and 178. The dark markings tend to be enlarged and more or less confluent, but occasionally are absent (Fig. 151). This form intergrades with the predominant eastern form (*quadrilineata*) by individual variation in some localities, and in some localities the predominant forms are intermediate in characters between the two forms.

A small, dark form occurs locally in the mountains of Colorado (Figs. 133, 166, 173, 178, and 181). The dark markings tend to be enlarged and confluent, and in extreme cases the body is almost wholly black and the fore wings are largely fuscous (Figs. 124 and 187). At the other extreme of the range of variation the insects are almost wholly pale (Fig. 155). A form that tends to be darker in general facies and slightly smaller in size than the Colorado mountain form occurs locally in the mountains of California (Figs. 137, 165, 171, and 184). These forms intergrade in characters with each other and with the *fascifrons* form.

A robust form with short, rounded vertex and yellow-veined, hyaline fore wings occurs in coastal marshes in Alaska (Figs. 129, 131, 172, 179, 180, and 186). Specimens resembling it from Michigan have been examined. It intergrades with the *fascifrons* form in characters.



Figs. 151-177. Head, pronotum, and scutellum of: *Macrosteles facifrons* complex. (Drawing to same scale).

On the lowlands of California pale forms with the dark markings absent or greatly reduced occur. Two such forms are shown in Figs. 152, 158, and 162 and Figs. 132, 156, 160, 163, and 164, respectively. They differ from each other in general facies of size and of shape of the vertex.

There are indications of the existence of forms additional to those mentioned

above, particularly in the southern and western regions of the United States, but the material available was insufficient for study.

Members of the complex are primarily of economic importance as vectors of various strains of *Calligenus callistephi* of Harris, a virus disease that produces the symptoms known as yellows or aster yellows in a great variety of plants: white-heart, rabbit-ear, or Rio Grande disease of lettuce; purple-top wilt, blue stem, or net necrosis of potato; and curly-top of ornamental plants. Both the *quadrilineata* and the *fascifrons* forms are among those that transmit the virus.

The nymphs feed on grasses and cereals in the spring, and may cause appreciable damage when abundant. In late spring the adults migrate to other herbaceous plants, where three or more overlapping broods develop during the summer. In late autumn the adults migrate back to grasses and cereals for the winter. It is not clear whether the winter is passed in the adult or in the egg stage. Specimens of the complex examined from:—Alaska; Canada: Alberta, British Columbia, Labrador, Manitoba, Northwest Territories, New Brunswick, Nova Scotia, Ontario, Quebec, Saskatchewan, and Yukon Territory; Mexico; Puerto Rico; United States: Alabama, Arizona, Arkansas, California, Colorado, Connecticut, Florida, Georgia, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, Nevada, New Hampshire, New Mexico, New York, North Carolina, North Dakota, Ohio, Oregon, Pennsylvania, South Carolina, South Dakota, Tennessee, Texas, Utah, Vermont, Virginia, Washington, Wisconson, and Wyoming.

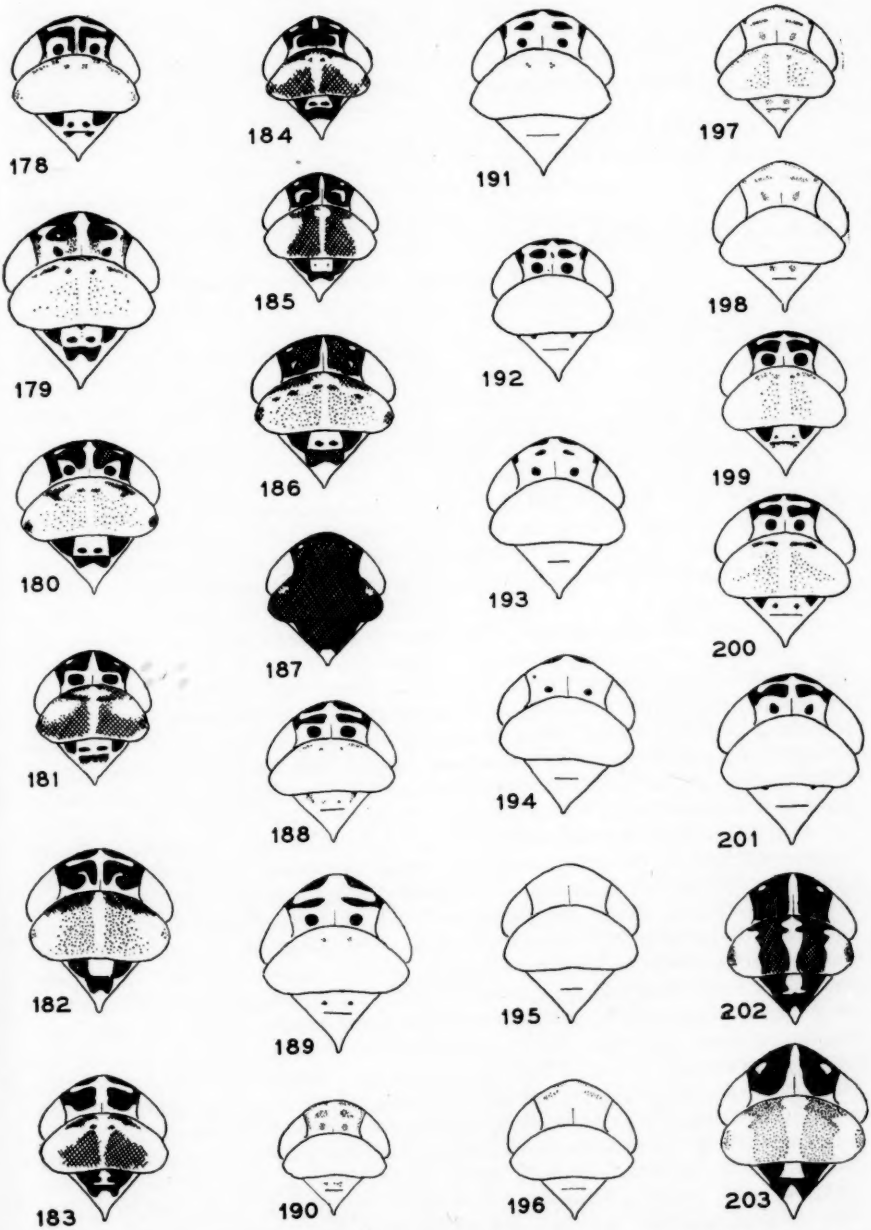
20. *Macrosteles* (*Macrosteles*) *cristata* (Rib.) complex

Figs. 27, 140-143, 190-195

Cicadula cristata Ribaut, 1927: 164.

This may be a complex of species that are poorly defined morphologically, like the *fascifrons* complex. Length 2.6–4.0 mm. General colour pale ochreous yellow, with black or brown markings. Fore wings whitish hyaline, tinged ochreous. There appears to be much variation. Specimens resembling the European specimens examined in genitalic characters—notably the broad apical processes of the aedoeagus (Figs. 142 and 143)—tend to have the dark markings reduced or absent (Figs. 193-195); these are from Wisconsin, Maryland, and Illinois. The dark markings are well developed in the European specimens. Another form, from Kansas and New York, has the dark markings well developed, the vertex more rounded (Figs. 190-192), and the apical processes of the aedoeagus more slender in ventral view and more nearly straight in lateral view (Figs. 140 and 141). One specimen of the latter form has the body and fore wings ochreous and the dark markings of the vertex orange-brown (Fig. 190). There are indications that the local and individual variation is extensive, but adequate quantities of material from different regions were not available for study.

M. cristata has not been recorded previously for North America. The characteristic feature is the dorsal flange on the shaft of the aedoeagus. Each of the apical processes of the aedoeagus is narrowed on its apical half. A tendency toward this is visible in some specimens of the *fascifrons* complex (Fig. 138), but otherwise it is characteristic of the *cristata* complex. Reliable characters for separating the females of the *cristata* complex from those of the *fascifrons* complex could not be found. The female also resembles those of *fieberi* and *curvata* but those species inhabit a different geographical region so that confusion is unlikely to arise. Specimens examined from:—United States: Arizona (Santa Cruz River near Tubac), Georgia (Peach Co.), Illinois (Algonquin), Kansas (six miles east of Yates Center, Woodson Co.), Maryland (Takoma Park), Texas (Devil's River and Concan), Wisconsin (East Troy), and Wyoming (Evanston).



Figs. 178-203. Head, pronotum, and scutellum of: 178-187, *Macrosteles fascifrons* complex; 188, 189, *M. laevis*; 190-195, *M. cristata* complex; 196-198, *M. obsoleta*; 199-201, *M. bifurcata*; 202, 203, *M. borealis*. (Drawings to same scale)

21. *Macrosteles* (*Macrosteles*) *laevis* (Rib.)

Figs. 28, 144, 188, 189

Cicadula laevis Ribaut, 1927: 162.

Length 3.5–4.0 mm. General colour pale ochreous, tinged greenish, with black or dark-brown markings. The fore wings are pale ochreous, tinged greenish.

This European northern and mountain species has not been recorded previously for North America. The form of the aedoeagus is distinctive. The female resembles somewhat *salina* and some forms of the *fascifrons* complex in shape of the head but can be distinguished by the form of the seventh sternite. Specimens examined from:—Alaska (Karluk).

22. *Macrosteles* (*Macrosteles*) *obsoleta* (Dorst)

Figs. 29, 148, 149, 196-198

Cicadula obsoleta Dorst, 1931: 42.

A small species, 3.0–3.5 mm. in length, but moderately robust. General colour fulvous yellow, with the dark markings, when present, reddish or brownish in colour and small in size; frequently without dark markings. Fore wings hyaline, tinged brownish between the yellowish-white veins.

The forms of the aedoeagus and of the seventh sternite of the female are distinctive. There is some variation in the degree of curvature of the apical processes of the aedoeagus, and in the degree of development of the spine on the inner margin of each process; in some specimens this spine is represented merely by an angle in the process. The aedoeagus of the holotype is shown in Fig. 148, and a paratype in Fig. 196. Specimens examined from:—United States: Florida and Texas.

23. *Macrosteles* (*Macrosteles*) *bifurcata* n. sp.

Figs. 146, 147, 199-201

Length 3.5–4.0 mm. Vertex rounded in front, relatively narrow between the eyes and hardly longer at middle than next the eye. Aedoeagus with apical processes long and stout, extending parallel with one another and in line with the shaft for nearly two-thirds of their length, then each bifurcating into a straight, tapering spine in line with the shaft and a longer spine that curves upward and outward.

General colour greenish-yellow with black markings. Posterior spots of vertex large and round; median spots expanded toward their inner ends and confluent laterally with the lateral spots; anterior spots large. Face with a pair of large, oval spots below margin of vertex, a dark median streak, dark lateral arcs, and the sutures broadly dark-marked. Pronotum more or less suffused brownish near anterior margin and on disc at each side of mid line. Scutellum with black basal triangles, a pair of spots on disc, and sometimes a dark suffusion on transverse impression. Abdomen black except at the lateral and posterior margins of the segments. Fore wings hyaline, usually more or less tinged smoky between the veins. Hind wings hyaline. Specimens from Snow Hill, Maryland, are pale ochreous in general colour with the fore wings hyaline whitish-ochreous, and have the dark markings of the body reduced.

The form of the aedoeagus is distinctive. The shape of the vertex of the male is rather distinctive, though somewhat resembling that of forms of the *fascifrons* and *cristata* complexes. The female could not be separated reliably from females of those species. Described from seven males. What may be females of this species have the vertex distinctly obtusely pointed and one-tenth longer at middle than next the eye (Fig. 201).

Holotype—♂, Arran Lake, Ontario, September 15, 1927 (G. S. Walley). No. 5981 in the Canadian National Collection, Ottawa.

Paratypes—♂, Bergen, New York, July 24, 1946 (R. H. Beamer); in mosquito trap, Snow Hill, Maryland, July 11 and 12, 1932 (F. C. Bishop); ten miles west of Annapolis, Maryland, September 18, 1932 (P. W. Oman) (two specimens); Algonquin, Illinois, August 1, 1895 (C. F. Baker Collection).

Holotype in the Canadian National Collection, Ottawa; paratypes in the United States National Museum, Washington, D.C.

24. *Macrosteles* (*Macrosteles*) *borealis* (Dorst)

Figs. 30, 125, 150, 202, 203

Cicadula borealis Dorst, 1931: 45.

Length 3.3–4.2 mm. General colour yellow with heavy black markings. Fore wing whitish hyaline, marked with brownish or blackish in the form of irregular, oblique, transverse bands. The species is fairly constant in colour and markings, the chief variation occurring in the intensity of the dark markings of the pronotum and fore wings. There is rarely a reduction in the size of the black markings of the vertex.

The form of the aedoeagus is distinctive. The dark markings on the head, thorax, and scutellum give the insect a striped appearance that is rather distinctive. It is mainly a Boreal and mountain species and appears to be local but common where it occurs. Specimens examined from:—Alaska; Canada: British Columbia, Manitoba, Northwest Territories, and Yukon Territory; United States: Michigan, Montana, and Washington.

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Note added in press:—Ossiannilsson (1951, *Opusc. Ent.* 16: 109-111) found specific characters in the apodemes of the second abdominal sterna of the males of European species of *Macrosteles*. This structure has not been studied in American species.

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